Agent-based modelling to improve management strategy evaluation in complex problems of biodiversity conservation

Adrian Bach

Thesis for the degree of Doctor of Philosophy

Biological and Environmental Sciences

School of Natural Sciences

University of Stirling

March 2023

Thesis abstract

Amid the Earth's 6th mass extinction, conservation of the remaining biodiversity is more urgent than ever. But conservation faces the many challenges associated with the management of ecosystems, including the different sources of uncertainty around their joint social and ecological dynamics. Moreover, mismanagement can have detrimental consequences for both conservation and people's livelihood. To help managers design efficient and equitable policies in such complex situations, the use of simulation models as virtual laboratories to evaluate management scenarios have become widespread. Yet, most of these models are mathematical models, which can be limited in conservation problems. Indeed, the latter are rather small-scale, often spatially explicit, and unexpected responses often stem from local interactions between the parts of the system. These features are key assets of agent-based modelling (ABM), which should therefore be more appropriate but is still scarcely applied in management strategy evaluation. In this thesis, I further develop the use of ABM in conservation by designing agent-based tools to evaluate alternative management strategies in two complex conservation problems: the management of conservation conflicts between species protection and agriculture, and the management of species endangered by apparent competition.

First, I address the timing of management intervention in a conservation conflict between a manager aiming to conserve an animal population and farmers aiming to maximize yield by protecting their crop from consumption by the animal population. Building upon the agent-based software *GMSE,* which simulates the budget-constrained adaptive management of conservation conflicts, I propose a novel management strategy that dynamically alternates between intervention and waiting based on the monitoring of the distance between the population density and manager's target. The evaluation shows that my strategy can produce at least as efficient and equitable results as unconditional intervention while allowing critical budget savings. This strategy is now available in the *GMSE* package to be evaluated in other cases of conservation conflicts and my method proposes a way to do so in a more equitable way.

Then, I introduce an ABM of trophic interactions between several species in several trophic layers in which apparent competition can emerge. I validate it in its essential version according to the ABM framework and discuss its adequacy with apparent competition theory. Overall, my model behaves as theory and empirical cases predict, with some interesting contradictions challenging predictions of previous mathematical models. The

model is now fit for the addition of more complex features needing further understanding in apparent competition theory and conservation.

Finally, I demonstrate how my model can be used to evaluate removal strategies to conserve a prey species endangered by apparent competition with an alternate prey species mediated by a shared predator. Predator removal only, alternate prey removal only, and simultaneous removal of the predator and alternate prey all successfully prevented the extinction of the endangered population, but the simultaneous removal strategy was the most efficient in conserving the endangered population while also ensuring more stable dynamics and higher densities of the other species. Any combinations of these removal strategies are now available in my model for evaluation by researchers or managers in other cases, and my method proposes to conserve the endangered population while also ensuring the persistence of the other species in the system.

Across these chapters, I demonstrate how the agent-based approach can efficiently integrate the complexity of conservation problems to produce informative tools for biodiversity management strategy evaluation. Notably through human individual decision-making, complex individual behaviour, and spatially explicit modelling along with the simulation of different sources of uncertainty. I have shown, with general examples, how to use the modelling tools I provide, with methods enlarging the scope of conservation objectives: a better consideration of the equity of management measures between conservation and land-users’ livelihood in conservation conflicts, and a better inclusion of management consequences on other species in interaction with the population of conservation interest. Through my models’ development and validation, I have questioned and enhanced the theory of conservation conflicts' adaptive management and of apparent competition’s underlying mechanisms and management.

Résumé de la thèse

Face à cette sixième extinction de masse, préserver la biodiversité qu'il nous reste est plus urgent que jamais. Mais conserver la biodiversité implique de surmonter les défis inhérents à la gestion des systèmes socio-écologiques complexes que sont les écosystèmes, et notamment les différentes sources d'incertitude qu'ils comportent. D'autant plus que des erreurs de gestion peuvent être délétères pour la biodiversité comme pour la vie des personnes impliquées. Pour assister les gestionnaires de biodiversité dans l'élaboration de politiques efficaces et équitables, il est désormais commun d'utiliser des modèles de simulation pour tester des scenarios de gestion. Cependant, la plupart de ces modèles sont dit 'mathématiques' ; une approche par équations qui peut montrer ses limites quant aux problèmes de conservation. Ces derniers étant plutôt à petite échelle, ayant des implications spatiales bien précises et dont les comportements inattendus proviennent souvent des interactions locales entre les parties qui les composent. Les modèles individu-centrés, plus mécanistiques, sont plus indiqués pour simuler ces aspects, mais cette approche est encore peu appliquée dans l'évaluation de stratégies de gestion en conservation. Avec cette thèse, je participe à la démocratisation de l'approche individu-centrée en conservation en proposant de nouveaux outils de modélisation pour évaluer des scenarios de gestion dans deux problèmes complexes de conservation : la gestion de conflits de conservation et la préservation d'espèces impliquées dans des interactions de 'compétition apparente'.

D'abord, je traite du timing d'intervention des gestionnaires dans un conflit entre la conservation d'une population animale et des agriculteurs voulant en minimiser l'impact sur leurs cultures pour garantir la rentabilité de leur exploitation. Sous la forme d'une nouvelle option dans le logiciel *GMSE*, qui simule la gestion adaptative de conflits de conservation sous contraintes budgétaires, je propose plusieurs stratégies basées sur le monitoring pour déterminer si une intervention est nécessaire ou si attendre est préférable. L'évaluation montre qu'une de mes stratégies donne des résultats au moins aussi satisfaisants qu'une intervention inconditionnelle, tout en permettant d'importantes économies de budget. Cette stratégie est désormais disponible dans le package *GMSE* pour une évaluation dans d'autres situations et ma méthode défend une évaluation équitable entre conservation et intérêts humains.

Ensuite, je présente le premier modèle individu-centré simulant les interactions de compétition apparente entre plusieurs espèces reparties sur plusieurs niveaux trophiques.

Je valide ce modèle dans sa version la plus essentielle dans le cadre de travail individu-centré avant de discuter de son adéquation avec la théorie en dynamique des populations et de réels cas de compétition apparente. Globalement, mon modèle se comporte comme attendu par la théorie et les études empiriques, avec quelques contradictions intéressantes qui mettent en perspective les prédictions des modèles mathématiques usuels. Le modèle est maintenant prêt à incorporer des mécaniques plus complexes pour répondre aux questions encore en suspens dans le domaine de la compétition apparente, ainsi que pour anticiper leur impact sur le succès des programmes de conservation.

Enfin, je démontre comment mon modèle peut être utilisé pour tester des scenarios de gestion pour la préservation d'une population de proie en danger d'extinction à cause d'interactions de compétition apparente avec une autre espèce de proie par le biais d'un prédateur commun. Les trois stratégies testées, (i) réduction de la population de prédateurs, (ii) réduction de la population de la proie alternative et (iii) réduction simultanée des populations de prédateur et de proie alternative, ont bien empêché la disparition de l'espèce en danger, mais la stratégie (iii) a montré de meilleurs résultats dans la préservation de cette dernière, tout en assurant la stabilité du système et une densité de population plus satisfaisante pour les autres espèces du système. Toutes les combinaisons de ces trois stratégies sont disponibles publiquement dans mon modèle pour évaluation dans d'autres cas de compétition apparente, et ma méthode assure la prise en compte de toutes les espèces impliquées.

Table of contents

Table of figures

Table of tables

Acknowledgements – Remerciements

To my supervising team: Jeroen Minderman, Aileen Mill, Nils Bunnefeld, A. Bradley Duthie, thank you all for convincing me that my work was publishable, for your help on the article's manuscript and the thesis plan. Special thank you, Nils, for inviting me on the field trip **in** Orkney. Beside reminding us of outside life after lockdowns, it has opened my eyes on the actual people behind the code and it was a real turn in the angle I intended to give to this PhD. Brad, it was a privilege to have such a brilliant researcher, a passionate scientist, and a sincerely kind person as a first supervisor. I am so grateful for the constant support, indefectible availability, and countless times when I have felt back on my feet and motivated to go on after a meeting with you. I am proud to, very respectfully, count you as a friend.

Even if the pandemic made this experience rather solitary, I want to say thanks to the BES lab, the ConFooBio team and my office mates. Special thank you to Joanne Clarke and Martina Quaggiotto for the cheerful carpooling, to Lynn McGregor for her patience and pedagogy, and to Scott Jackson for preserving my ability to run simulations remotely. Thanks to NERC and IAPETUS for funding this research. Finally, many thanks to the SEABOOST people and to Marc Bouchoucha for hosting my placement.

I am grateful to the fantastic, passionate scientists that gave me the taste for research during my studies: Marine Cambon, Audrey Dussutour, and Jerome Bulh, thank you so much for giving me my chance and taking me under your wing.

Un grand, grand merci à mes ami·es, pour me faire rire fort en groupe, soutenir en privé, et pour ces moments de légèreté qui redonnent du souffle ; j'aimerais vous citer toutes et tous ! Gros big up à mes coffres forts Antonoar, Valentype, Yassoin, Larasse, Clémouze, pour avoir été là dans les passages difficiles. One special for you Josh, best mate to complain with, go to music and talk with for hours. Et petit traitement de faveur pour toi aussi Joss, qui a donné beaucoup de force dans les derniers mois de la thèse par ta fraicheur, ton énergie sans limite et ton rire tonitruant.

Merci à la famille, la mienne et celle qu'on me prête, Estelle, Nathalie, pour ta sagesse et tes conseils, Bernadette, Jean-Marc, Élie, Richard et Mamie Tina, solide comme le roc. Une pensée également pour Mamie Trini et mon père Gilou, j'espère que vous seriez fier·e. Et bien sûr Mercedes, merci Maman pour ton amour et ton dévouement depuis le jour 0.

Flora, comment te dire. Merci pour ton amour inconditionnel et ta douceur, merci de supporter mes états d'âme avec attention, d'être ma meilleure avocate, pour toutes ces fois où je suis l'homme de Flora Fettah dans des lieux incroyables, merci de rendre le quotidien si beau, tout en menant a bien tes projets, en poussant tes luttes et en devenant la most wanted de ton domaine. Je n’aurais pas pu amener cette thèse au bout sans toi. Vivement la suite !

1. General introduction

1.1.The urgency to conserve biodiversity

Biodiversity, or the living part of nature, is one of the nine planetary boundaries, defining the environmental limits within which humanity can thrive safely as a species (Steffen *et al.*, 2015). Indeed, the higher the functional, specific, genetic diversity in living being populations, the stabler and more resilient the ecosystem they belong to (Allesina and Tang, 2012; Hautier *et al.*, 2015). We need healthy ecosystems because humanity's survival crucially depends on the services they provide, such as pollination, soil enrichment, water treatment, carbon dioxide fixation, among many more (Costanza *et al.*, 1997; Bennett *et al.*, 2015). However, ever-growing human activities poses a major threat to biodiversity, to such an extent that the current proportion of declining species in certain species groups is comparable to Earth's previous mass extinction episodes (Ceballos, Ehrlich and Dirzo, 2017). Conjointly with addressing the very sources of this noxious impact, the conservation of the remaining biodiversity is more urgent than ever.

1.2.The challenging complexity of biodiversity conservation

Biodiversity conservation faces many challenges. Ecosystems form densely interconnected systems involving multiple interactions between its parts and include properties such as feedback loops or non-linearity. Such complexity makes it very difficult to anticipate the entirety of the consequences of human intervention on natural populations and/or landscapes (Keith *et al.*, 2011; Redpath *et al.*, 2013; Game *et al.*, 2014; Mason, Pollard, *et al.*, 2018). Additionally, the total area used for human activities is increasing and often overlaps with the ranges of species of conservation interest, and intervention therefore also has an impact on human livelihood. Factors increasing the difficulty of decision-making in conservation include the uncertainty surrounding the mechanisms at stake in the populations *(model uncertainty)*, how the environment influences their dynamics (*process uncertainty*), the accuracy of the measures/observations realised on the field (*observation uncertainty*), the response of population and people to a conservation policy, and even the extent to which it will actually be applied (*implementation uncertainty*) (Williams, Johnson and Wilkins, 1996; Bunnefeld, Hoshino and Milner-Gulland, 2011; Keith *et al.*, 2011; Nuno, Bunnefeld and Milner-Gulland, 2013; Nicol *et al.*, 2019). Also, there is a large variety of conservation methods, should they be indirect, such as legislation (e.g., species protection, restrictions on harvest), establishment of restricted access areas (van Wilgen and Biggs, 2011; Nuno, Bunnefeld and Milner-Gulland, 2013; Ng'weno *et al.*, 2019), impact offsetting (Gordon *et al.*, 2011), species reintroduction (DeCesare *et al.*, 2010; Krofel and Jerina, 2016;

Behr, Ozgul and Cozzi, 2017); and direct, such as species removal (Roemer *et al.*, 2001; Roemer, Donlan and Courchamp, 2002), distribution of culling licences (Courchamp, Langlais and Sugihara, 1999; Mason, Keane, *et al.*, 2018), or offspring control (Pollard, 2018). Finally, mismanagement can have unexpected detrimental, sometimes irreversible consequences, including population extinction, dysfunctional ecosystem services, loss of income for land-users, or impact on food security (Kaswamila, Russell and McGibbon, 2007; Redpath *et al.*, 2013, 2015). Consequently, how do conservation managers make decisions on the best intervention to protect biodiversity facing such challenges? How can they choose the most adapted, effective, safest measure, or combination thereof, avoiding adverse consequences for ecosystems and their human component while embracing uncertainty? Which action should be prioritised? There are two widespread tools to overcome such challenges. On the one hand, there is adaptive management, warranting the implementation of policies that are updated and improved iteratively by learning from its outcomes through regular monitoring (Williams, Johnson and Wilkins, 1996; Keith *et al.*, 2011; van Wilgen and Biggs, 2011). On the other hand, there is the use of simulation models to improve predictions on a policy outcome before its implementation or update.

1.3.Models as decision-helping tools

The use of simulation models in ecology was often disregarded before the 90s because of a supposed opposition and/or scientific inferiority to empirical experimentation, but it is now more widely acknowledged that both approaches participate, sometimes in an intertwined manner, to ecological knowledge (Caswell, 1988), and these models have become widespread in natural sciences (Judson, 1994; Grimm, 1999; Bousquet and Le Page, 2004; Heinonen and Travis, 2015; Holt and Bonsall, 2017). Simulation models predict the evolution of a given system over time based on specific sets of assumptions and hypotheses that are modulated by parameters. In conservation science, these models usefully simulate most of the processes causing the challenges presented in the section 1.2. Population dynamics can be simulated over time as the combination of life events such as birth, death, alimentation, predation, migration (Holt, 1977; Abrams, Holt and Roth, 1998; Chesson, 2000). Environment variability can also be modelled, along with its effect on population dynamics (Holt and Barfield, 2003; Barraquand *et al.*, 2015). Uncertainty can be simulated in models by introducing stochasticity, i.e., randomness, in the processes modelled, through the use of probabilistic processes, allowing parameter values to vary randomly, or replicate stochastic simulations a number of times to explore different possible outcomes (Roemer, Donlan and Courchamp, 2002; Bunnefeld, Hoshino and Milner-Gulland, 2011; Glynatsi, Knight and Lee, 2018; Nilsson *et al.*, 2021). Monitoring uncertainty can also be simulated by models (Nuno, Bunnefeld and Milner-Gulland, 2013; Duthie *et al.*, 2018), and significant progress has been made in simulating the behaviour of human stakeholders in conservation problems using game theory (Colyvan, Justus and Regan, 2011; Tilman, Watson and Levin, 2017) and, more recently, artificial intelligence (Duthie *et al.*, 2018; Kamra *et al.*, 2018; Cusack *et al.*, 2020; Nilsson *et al.*, 2021). Combining these with the simulation of conservation policies or scenarios, one can evaluate the efficiency of management in a particular situation given a conservation goal and provide arguments for policy making, this method is known as Management Strategy Evaluation, or MSE (Smith, Sainsbury and Stevens, 1999; Bunnefeld, Hoshino and Milner-Gulland, 2011; Milner-Gulland, 2011; Bunnefeld *et al.*, 2013).

1.4.Usual modelling approaches: advantages and shortcomings

1.4.1. Population dynamics

The usual, historical way to simulate population dynamics is with Ordinary Differential Equation (ODE) systems. An ODE is a mathematical equation modelling change in population density (often denoted dX, X being the population density at a given time) over a short period of time (often denoted dt) according to the life events assumed to affect population change. Most of the time, the life events are modelled as functions of X modulated by parameters in a way that reflects density-dependence. By having one ODE per species present in the system, life events can also be functions of the densities of other species within the broader community, thus simulating species interactions. By solving such an ODE system, it is possible to predict the density of each species at a given time for a given set of parameter values and density in a preceding time. The most widespread version of an ODE system for directly interacting species is the Lotka-Volterra population model (Lotka, 1920; Volterra, 1926), connecting ${dX}/{dt}$ to births and deaths functions. By shaping these functions and setting the associated parameter values, one can adapt this model to a wide range of direct interaction systems, especially trophic dynamics (Holt, 1977; Chesson, 2000). This model was later generalised to direct and indirect interactions by McArthur and Rosenzweig (Rosenzweig and MacArthur, 1963), also known as Lotka-Volterra competition model, making it more practical for modelling several types of interaction in multi-species communities (Chesson and Kuang, 2008; Serrouya *et al.*, 2015; McPeek, 2019).

One shortcoming of this model is that it cannot easily account for population structure, in the sense of different dynamics according to the age, or developmental stage of an individual or subgroups within a species. For problems with population structure, matrix models are more appropriate; Leslie model (1945) being the most usual. In such models, a population is defined by a vector in which elements are the densities of individuals in each life stage. To compute the densities at a given time, the population vector is multiplied by a squared matrix of the same size as the vector, in which elements are transition coefficients from one stage to another or among a same stage (Bunnefeld *et al.*, 2013; Wam *et al.*, 2016). This approach is particularly useful in invertebrate ecology, where animals have very different dynamics according to their developmental stages (Mouquet *et al.*, 2005).

One advantage of these kinds of models is that mathematics facilitates the analysis of stability, at least with only two to three species in the system. This analysis predicts the behaviour of the system in the long term in absence of perturbation, i.e., at equilibrium, according to the parameter values (Volterra, 1926; Holt, 1977; Holt, Grover and Tilman, 1994). Indeed, these models are deterministic, meaning that the same set of initial conditions and parameters will always result in the same prediction, even in the long term. This can appear as a shortcoming in conservation science because actual population dynamics are far from deterministic; they are subject to different levels of inter-individual variability and to a myriad of external perturbations from their environment. In fact, the existence of equilibrium states in populations dynamics are dependent on very specific assumptions, which are seldom verified in the field (Grimm, 1999; Chesson, 2000; DeAngelis and Grimm, 2014; Stillman *et al.*, 2015).

With these approaches, uncertainties can only be accounted for in an extrinsic manner, in the sense that one must change the model somehow and compare to include uncertainty. In theory, in ODE systems, the model uncertainty, or the uncertainty surrounding the understanding of the mechanisms at stake in the population, can be assessed by changing the shape of the life event functions and assess the impact on the densities predicted. With a given choice of model, model uncertainty also lies in the values estimated for parameters, which can be assessed by varying these values by a certain amount and then compare the impact on the densities predicted. For example, in a derivation of a Lotka-Volterra model simulating the golden eagle-mediated apparent competition between the endangered island fox and introduced feral pig populations on Californian islands, Roemer, Donlan and Courchamp (2002) estimated which parameter was the most impactful by independently varying the parameter values by ±10% and measured the change in the predictions. This determined which parameter values had to be the most accurately measured or estimated, while uncertainty around the other values might have less impact on predictions. The observation uncertainty, or the uncertainty around the accuracy of measurements carried out on the field, can be assessed using a similar method: varying the initial population densities provided to the model by a certain amount and measuring the impact on the prediction. In principle, the model and observation uncertainties could be accounted for by allowing the parameter values and densities to vary at random within a certain range, the size of which corresponding to the level of uncertainty, and repeat simulations to have a range of possible outcomes (Bunnefeld *et al.*, 2013). This is a way to make predictions while embracing uncertainties and draw conclusions even if the parameters or the densities are not set to their 'true' values, but it is still rarely applied in conservation. This shows how the traditional mathematical models for population dynamics are not best suited to account for the uncertainty at stake in conservation problems.

The top-down approach of these mathematical models is theoretically better suited to general, large-scale questions where the impact of individual-levels interactions can be safely ignored, which is increasingly unlikely as conservation problems get more complex than mere population dynamics. Another shortcoming is that the models presented in this section are spatially implicit by nature; all life events happen at the same time at a global level, leaving few options to include spatial or temporal variability. This prevents the simulation of several geographical conservation measures such as fencing (Kaswamila, Russell and McGibbon, 2007; Nyhus, 2016; Pooley *et al.*, 2017), providing shelter (Jensen, Wisz and Madsen, 2008; Rakotonarivo, Jones, *et al.*, 2021), or installing supplementary feeding sites (Krofel and Jerina, 2016). The fact that all life events happen at the same time also makes questions about the timing of intervention of biodiversity managers more complicated to model.

1.4.2. Environmental variability

Simulating environmental variability is a way to account for process uncertainty in predictions. It is usually simulated by a change in model parameter values that are independent of population dynamics or conservation actions. By allowing changes in the parameters linked to mechanisms that can be influenced by environmental variations, predictions can be made considering these potential perturbations. For example, Holt and Barfield (2003) modelled environmental variability in a three-species Lotka-Volterra system of apparent competition by changing the parameter values according to a sinusoidal function oscillating around a fixed value. The frequency of the sinusoid represented how often variations are observed and the amplitude represented the intensity of fluctuation in the parameter values. The study showed that strong fluctuations affected species persistence in their apparent competition model, with different impacts according to which parameter value varied. Another example is in *RangeShifter*, an agent-based model simulating population range expansion according to genetics, population dynamics and landscape characteristics on landscape maps (Bocedi *et al.*, 2014, 2021). In this model, the authors simulated environmental variability by allowing some landscape cell characteristics to change stochastically in two ways. First, the authors introduced a small probability of a cell's population extinction, thus modelling unexpected perturbations or interventions resulting in the local extirpation of the population. Second, they allowed the carrying capacity of the landscape cells (the maximum number of animals that the landscape resources can sustain) to vary seasonally to account for the variability in resource availability between winters and summers. The simulation of such variability makes predictions more robust to uncertainty around the likelihood of environmental perturbations that could hinder conservation.

1.4.3. Stakeholders' decision making

Game Theory (GT), introduced by Von Neumann and Morgenstern in 1944, has been the leading framework for decision-making modelling historically. Myerson (1991) described GT as follows: "*the study of mathematical models of conflict and cooperation between intelligent rational decision makers [which strategies] affect one another's welfare*". In these games, the players act in order to maximise the expected value of their outcome from the game, the so-called utility. Utility is not necessarily quantified as a monetary pay-off; it can be seen in many ways, e.g., time, effort saved, well-being, happiness, etc, or a mix of them. A game theoretical perspective can provide insights about "*the strategies different stakeholders will likely adopt given their objectives, […] the range of possible outcomes, […] and whether an optimal or satisfactory solution for all stakeholders can be reached simultaneously*" (Colyvan, Justus and Regan, 2011). It was first used in biology in the landmark paper "The Logic of Animal Conflict" by Maynard-Smith and Price (1973), which modelled the dynamics of strategies in animal conspecific fights. Animal players were choosing between run-away, intimidating, and aggressive behaviours according to an opponent's behaviour in attempt to maximize their individual evolutionary pay-off. By solving game-theoretical systems as a pay-off optimisation problem, numerous studies investigated the evolution of the proportion of co-operators and defectors in common-pool resource games (exploitation of a resource, out of which each player wants to make the best pay-off). A co-operator's strategy is usually to share their pay-off to exploit less resources for a reasonable utility per capita, while a defector's strategy is usually to exploit the resource as much as possible to maximize a pay-off they do not share. In these studies, solving this game showed that the proportion of defectors and co-operators in a group of exploiters is very sensitive to different aspects like the size of the group or sub-groups (Hauert, Holmes and Doebeli, 2006), how fast the resource depletes (Hilbe *et al.*, 2018), or which type of sanction is applied to defectors (Tilman, Watson and Levin, 2017). More specifically for conservation, Colyvan, Justus and Regan (2011) applied the four main types of games in GT (simple, chicken, stag, and prisoner games) to adaptive management of a resource under protection, but its actual implementation in conservation problem is fairly novel. Recently, Glynatsi, Knight and Lee (2018) used GT to model a conflict over rhinos protection and illegal poaching of ivory as a common-pool resource problem. According to poachers being unconditional or selective killers, they assessed which proportion of rhinos should be de-horned to minimize their killing. These GT models do not generally account for implementation uncertainty, but I could see it simulated by allowing the proportion of players using each strategy to vary stochastically, modelling some suboptimal choices in the population, although I am not aware of any example of such incorporation of uncertainty in GT models of conservation. The Game Theory framework is useful to simulate decision-making, but it can have limitations when applied to complex conservation problems.

Indeed, in GT, the behaviour rules guiding decision-making are fixed, with finite sets of actions (e.g., cooperate or defect, rock-paper-scissors) and the players are assumed perfectly rational and aware of the best options for them (Myerson, 1991). Human decision-making is not perfectly rational, and the lack of dynamic stakeholder behaviour modelling has been identified as a major cause of failure in conservation (Schlüter *et al.*, 2012). In conservation, the panel of options is usually larger than tractable by game theoretical problems, and agents must often make a choice over a continuum of possible actions (Duthie *et al.*, 2018; Kamra *et al.*, 2018; Cusack *et al.*, 2020). In a more flexible way, decision-making can be simulated by computing the utility of a given strategy according to different criteria. In Termansen *et al.* (2019), the authors used a random utility approach to simulate farmers' decision-making in a problem of land allocation to sheep grazing or heather burning for grouse keeping in the UK. Farmers decision was simulated by a probability to choose a strategy among the ones that a management policy allowed, by maximising utility according to the value each farmer gave to sheep stock and heather diversity, to expected environmental change and to expected changes in policy, modulated by a stochastic error term to simulate variability in decision making. But people do not always make the best choices (even according to their values), and they often cannot consider all the possible outcomes or solutions to a problem. Artificial intelligence offers another angle to simulate human decision-making by mimicking errors and learning from past mistakes but is still quite scarcely applied to modelling human decision-making in conservation science.

Among the few examples in literature, the software *GMSE* (Duthie *et al.*, 2018) and subsequent works using it (Cusack *et al.*, 2020; Nilsson *et al.*, 2021; Bach *et al.*, 2022) features an evolutionary algorithm (Hamblin, 2013), a form of artificial intelligence simulating manager's and land-user's decision-making. Combined with an individual-based approach, it models decision-making independently for each stakeholder with the possibility for sub-optimal choices along a continuous set of possible actions. But this algorithm cannot learn by construction.

Use of Machine learning to predict decision-making in conservation problems is even rarer, but Kamra *et al.* (2018) presented a continuous strategy game, in which strategies are defined by values on different continuous action scales and players could optimise their strategies through machine learning. The game consisted in forest defenders protecting a forest from lumberjacks wanting to log it. The forest was a circular map with trees randomly distributed from a forest centre, and players policies were sets of coordinates for each agent to place on the map. For a given randomly generated forest, they simulated the situation a thousand times and selected the policies that resulted in the best pay off for each player after ten rounds as the 'best response'. This was repeated for several different forest maps, hence generating a data set of forest maps with associated best response. Then, the authors designed a convolutional neural network taking a forest map as an input and outputting a mean and a standard deviation for defenders and lumberjacks, from which the agents' coordinates should be sampled from. The network was trained on a part of the data set to be able to predict policies as closely as possible to the 'best response'. The rest of the data set was used to test the neural network on forest maps it had never been presented to before and evaluate the accuracy of the prediction against the 'best response'.

This approach could be transferred to land-use decisions. A neural network could take a landscape as input, in a shape of a 3D matrix (like RGB images), the first layer being the land-use information, the second the prevalence of resources and the third an information on the policy. The output could be a layer with each argument being the action undertaken by the users on each of its land cells. Or, more complicated, a set of parameters for a given distribution in which users could draw a value (for example a number of animals to remove or scare) for their strategy. This network could be trained on the actions the stakeholders undertake in real-world cases. The good thing is that this training set would not necessarily be the most optimal policies given the situation, so the neural network would still be able to replicate the fact that humans do not always make the best choice (implementation uncertainty). Yet, the tractability of such a solution is arguable. The main problem being the size of the training data set; neural networks need a very large number of examples of one specific situation to reach maximum capacity (convention is at least 10000 examples for the training set in image recognition). This will be a problem in conservation because, with such complex situations, it is already complicated to find several examples of an exact same situation. A solution, already implemented by Rakotonarivo, Bell, *et al.* (2021) and Rakotonarivo, Jones, *et al.* (2021) would be to design a specific behavioural game structured in a way that could be learnt by a Neural Network and have as many stakeholders playing it to obtain a training data set. But even so, the games might need to be simulated, like in Kamra et al. (2018), to generate enough uncorrelated examples.

In conclusion, simulating decision-making along with its sources of uncertainty allows to predict management outcomes even if managers do not always make the most efficient policies and if stakeholders do not always behave as they are expected to.

1.4.4. Monitoring

The monitoring of the system under management is critical in conservation, and even more in adaptive management, because the decisions are made based on information measured on the field (Williams, Johnson and Wilkins, 1996; Keith *et al.*, 2011; Game *et al.*, 2014), on both the managed population and the people involved (Milner-Gulland, 2011). Therefore, the uncertainty associated with these measures can have a great impact on the efficiency of conservation policies and each monitoring methods has its own uncertainties associated. Here too, modelling can help in several ways.

Simulation modelling can help assess the uncertainty associated with a monitoring method. For example, Nuno, Bunnefeld and Milner-Gulland (2013) estimated the uncertainty associated with systematic reconnaissance flight surveys (an aerial, photographic, transect-like method used in the Serengeti reserve in Kenya) of wildebeest and impala populations according to sampling effort, species aggregation and observer error. The authors simulated the population distribution on a spatially explicit lattice as the 'true' population size, with both juveniles and adults. Then, the sampling method was simulated according to different population aggregation parameters, different distances between flight transects and different photograph frequencies. The simulated sampling was then compared to the true population size for each combination, thus providing an estimation of the best accuracy-to-sampling-effort ratios.

When modelling the conservation process with decision making, the uncertainty associated with monitoring, and therefore its impact on manager decisions, can then be simulated. In a study of budget-constrained conservation of protected fish against illegal fishing, Milner-Gulland (2011) explored the trade-off between the monitoring of a managed population size and the monitoring of illegal fishing for law enforcement, according to the level of the financial penalty for defection. The 'true' population was modelled with an ODE of logistic growth, and fishers chose between complying or poaching according to an effort-to-risk trade-off. The observation accuracy varied according to the budget allocated to monitoring. This 'virtual ecologist' study showed that monitoring accuracy of the fish population should be favoured when the fine is high, and the fishers' monitoring accuracy should be favoured when the fine is low, thus increasing conservation value before policy implementation. In the conservation-conflict simulation software *GMSE* (Duthie *et al.*, 2018), the monitoring accuracy of several sampling methods (including transect sampling, mark and recapture, or positional observation) can be parameterised, allowing managers to test and include the impact of the level of observation uncertainty on conservation outcomes.

Monitoring uncertainty can have an important impact on decision making, and therefore on management efficiency, and it can represent an important budget investment according to the method and accuracy needed to effectively monitor. Modelling is of great help to target the most efficient sampling method and dimension the sampling effort according to the conservation case, and therefore can avoid a long, expensive, and potentially harmful trial and error process on the actual populations.

1.4.5. Management scenarios

Following model development for the population dynamics, human stakeholders' behaviour, observation methods, and environmental variability, management scenarios are then simulated to evaluate their efficiency.

Conservation policies can be simulated in a fixed fashion to simulate real-world management strategies, i.e., once the policy is applied, it does not change over the evaluation period (Milner-Gulland, 2011; Glynatsi, Knight and Lee, 2018). Courchamp, Woodroffe and Roemer (2003) simulated, in a derived Lotka-Volterra ODE system, the management of the endangered island fox preyed upon by the protected golden eagle and involved in apparent competition with the introduced feral pig population. The authors simulated different removal policies of the eagle and pig populations by adding a density independent mortality in their equations, modulated by a removal rate parameter controlling the intensity of the removal policy for each species. By varying these parameters and assessing the fox population final density, the authors could provide guidance for policy making. Conversely, in a model for the protection of the Kenyan mountain Nyala antelope from poaching (Bunnefeld *et al.*, 2013), the managers set a harvesting quota that hunters should not exceed to keep the Nyala population to a level guarantying persistence. There were three alternative harvest quotas modelled: a fixed quota, a proportional quota (as in the previous example) and an adaptive version with a quota varying according to the change in the Nyala population between two monitoring instances. By subtracting this quota to the densities simulated in the Leslie population model, including a variable level of poaching by non-compliers, the authors could recommend an optimal harvest quota according to the level of poaching and model uncertainty. This common type of control strategy is often referred to as harvest control rules and sets removal quotas for human harvesters and/or financial penalties for non-compliers (Kell *et al.*, 2007; Milner-Gulland, 2011). Both are simulated in the software *FLR* (Kell *et al.*, 2007) where the interaction between fishing equipment's harvest quotas and the fine for over-fishing influence the fish stock in a defined maritime area. The quota and fine can then be optimised to ensure that the fish stock stays over a critical value. This idea can be applied to the distribution of human activities on a natural area, as in Wam *et al.* (2016) with the simulation of the management of a boreal forest generating value from logging, hunting and grazing areas. The authors posed this situation as an optimisation problem and tested several strategies to make the most out of the boreal forest, including maximising the utility of logging, of hunting, of grazing, or optimise the combination of them. By calculating the utility of each strategy based on the market prices of each activity, the authors presented an optimal repartition of the activities on the areas, controlling for the potential conflicts between land-user stakeholders (see also Chapman *et al.* (2009)). Yet, the methods presented here do not always fit in the adaptive management framework, where the policy is supposed to be updated and improved iteratively through regular monitoring of the outcomes.

Conservation strategies can be simulated in a more adaptive way according to monitoring. Already mentioned in the previous paragraph, the harvesting quotas can vary according to change in the managed population (Bunnefeld *et al.*, 2013). Nilsson *et al.* (2021) used the agent-based software *GMSE* (Duthie *et al.*, 2018) to model the management of the conservation conflict between agriculture and the protection of the crop-grazing common cranes in Sweden. Here, management strategy was modelled as a cost that farmers 'pay' to cull or scare cranes on their land. According to the distance between the monitored crane density and a target density chosen to ensure the population persistence, the manager sets these costs in the hope of influencing farmers behaviour towards cranes. Through simulations, the authors found the levels of subsidies that maximised both crane population size and farmer income.

These are all examples of how the simulation management scenarios helped assessing the efficiency of alternative strategies in a virtual environment and inform policy making. Now that modelling of population dynamics, monitoring, decision-making, and management strategies have been reviewed, how can models simulate the interaction of these features to assess the impact of conservation on a natural system?

1.4.6. Management strategy evaluation software

The MSE method warrants the investigation of the interaction between the natural, observational, human, and managerial components of a conservation problem to understand and anticipate its consequences on biodiversity and human livelihood. As we have seen in the previous section, modelling is a powerful tool to simulate all these aspects of social-ecological systems. Yet, building a model from scratch, for each new conservation problem, and, furthermore, make models of different aspects of conservation communicate to be used simultaneously, might be very costly in time and research investment, especially under the urgency to act and the increasing number of conservation problems that we will face. That is why some researchers in conservation and modelling have developed software combining sub models of these different aspects in a way that they can match a variety of cases when parameterised accordingly, without having to code new models all over. The software *ISIS-fish* (Mahévas and Pelletier, 2004) simulates the interaction between fish stock variations with complex population structure and temporality (Leslie matrix), fishing effort according to different types of fishing fleet, and management in the form of fishing quotas by fleet type, on a lattice map that can be filled to resemble a given maritime area. By testing and evaluating different management scenarios according to fishing effort and population dynamics, *ISIS-fish* can inform policy makers to implement the quota that will best trade-off fish stocks and fishing income. In a similar spirit, *FLR* (Kell *et al.*, 2007) simulates the same dynamics but includes the option for financial penalties in case of overfishing, and an observation model that can simulate monitoring error and uncertainty according to the different methods. To date only applied to terrestrial cases of conservation conflicts (Cusack *et al.*, 2020; Nilsson *et al.*, 2021; Bach *et al.*, 2022), the software *GMSE* (Duthie *et al.*, 2018) simulates the interaction of agent-based sub models of a population dynamics, monitoring with error and uncertainty, manager decision making and land users adaptive decision making along continuous set of possibilities for several different actions, all informing each other on the same agricultural landscape. The software allows its users to track the population density, the manager and land users' budgets and land users' income (see Chapter 2 for a detailed description). This model thus evaluates alternative adaptive management strategies while controlling for the equitable repartition of the costs and benefits of conservation between managers and land users in situations of conservation conflicts.

Importantly, the combination of models of ecological processes, human decision-making, and management strategies, that are already independently intricate, increases the overall complexity of the MSE software. It requires more parameters to calibrate, which makes the parameterisation of the model more challenging. More mechanisms also mean a more difficult communication of the model rationale and results to stakeholders. This can potentially hinder stakeholders' trust in the model and, ultimately, their will to engage with the model. That is why MSE software must find trade-offs between complexity, flexibility, and decision-helping potential for conservation.

A few notable examples aside, the overwhelming majority of models in conservation apply mathematical rather than agent-based approaches. Nevertheless, mathematical models can show their limits as the complexity of the problems increases while the agent-based approach might be theoretically more appropriate. I develop this argument and discuss agent-based modelling for conservation in more detail in section 1.5.

1.5.The agent-based approach

1.5.1. Switching point of view

Agent-Based Models, or ABMs, are also referred to as Individual-Based Models (Stillman *et al.*, 2015), Multi-Agent Simulation (Bousquet and Le Page, 2004), or Individual-Oriented Models (Uchmański and Grimm, 1996) in the ecology literature. This approach models a given phenomenon as a consequence of the interactions between its lower-level elements rather than describing the phenomenon as a whole using mathematical functions. Focusing on the lower-level elements allows a higher degree of complexity and a larger variety in interactions than usual mathematical models (MMs). ABMs can be seen as applying a bottom-up philosophy as opposed to top-down in MMs (Grimm, 1999). In this section, I argue about how this approach can better suit complex conservation problems.

In population dynamics, the focus changes from the population density fluctuations to the life history of individual animals themselves. In ABMs, the density is not modelled explicitly, it is simply the sum of the living animals. Instead, the life events (birth, death, feeding, moving, reproduction, etc.) are modelled explicitly for each animal independently. In MMs, the state variables (or the physical values that describe a phenomenon) are described as the results of the dynamics of an average individual population, in proportions. During a timestep, a fixed proportion of such population will die, a fixed proportion will be attacked, a fixed proportion will be transformed into offspring, and so on to obtain a proportional change in density according to the preceding timestep (the growth rate). This change of focus is reflected in the nature of the model's parameters, that switch from population-level proportions and rates in MMs, to probabilities and values for individual traits in ABMs. For example, the reproduction probability can be the same for a whole population, but the realisation of reproduction will depend on individual animal trials. With such probabilities, it is impossible to predict if a given animal will reproduce or not, if it will survive or not, or how far it will move. This offers a more mechanistic, more realistic way of modelling that naturally generates inter-individual variability in population dynamics, therefore intrinsically simulating the 'model uncertainty'. In a review of advances in ABMs in ecology, DeAngelis and Grimm (2014) provide a good illustration of the fundamental difference in modelling animals' as individuals instead of modelling densities explicitly: "*one single population size may represent completely different distributions of individuals' attributes which will surely have enormous consequences for population dynamics* ".

Importantly, switching focus towards animals also allows the modelling of a higher level of complexity in species life cycles. By modelling each animal explicitly, individuals can have their own 'age' and life events can be made dependent of it. Indeed, as explained by Uchmański and Grimm (1996), the dynamics in different life stages of a given species are sometimes more distinct than the same life stages of two separate species. MMs such as matrix population models can simulate different dynamics for different life stages (Leslie, 1945; Mouquet *et al.*, 2005; Bunnefeld *et al.*, 2013), but the focus is still on density as a whole and the parameters are still rates. This is of particular importance, for example, for fisheries management where the fish stock heavily depends on the very distinct dynamics at the juvenile stage, notably predation and interaction with other species in the nurseries (Mahévas and Pelletier, 2004; Kell *et al.*, 2007; Bouchoucha, 2016; Bouchoucha *et al.*, 2016).

Uchmański and Grimm (1996) and DeAngelis and Grimm (2014) argue that the explicit modelling of resource availability is also a key feature that characterises the ABM approach. Modelling the dynamics of a primary resource is possible with ODE systems (Holt, 1977; Holt, Grover and Tilman, 1994), but the specificity of ABMs allows each animal to differ from its conspecific in resource acquisition (due to inherent difference in foraging efficiency or to stochasticity in resource quality or abundance) hence generating intrinsic interspecific competition. Interspecific competition can also be simulated in ODE systems with Lotka-Volterra equations, usually by using a logistic growth equation for the non-predator species and modulating the value of carrying capacity to represent self-limited growth rate. In a more explicit way, the Lotka-Volterra competitive model simulates interspecific competition in the form of a reduction of the growth rate according to a fixed coefficient and to the population density (Abrams, 1980; Chesson and Kuang, 2008; Orrock, Holt and Baskett, 2010; Serrouya *et al.*, 2015; McPeek, 2019). Again, the focus is global and there is no acknowledgement of the inter-individual differences in foraging efficiency, nor of the complexity of the relationship between resource abundance heterogeneity and intraspecific competition. By modelling resource dynamics explicitly as a currency, the impact of environmental perturbations on population dynamics can be predicted more accurately through the alteration of resource availability or foraging behaviour (Stillman, 2008; Bocedi *et al.*, 2014, 2021; Railsback, Ayllón and Harvey, 2021).

1.5.2. Complex behaviours

ABMs expand the possibilities for modelling animal behaviour, notably foraging strategies. Modelling animals independently allows the simulation of active foraging behaviour by making animals drawn to areas of higher concentration of their resources, or to potential mates, and affect the distribution and aggregation of animals on a landscape (developed in more details in section 1.5.4). This can have strong implications for predator-prey dynamics as local aggregation can increase predation pressure (Schmitz and Booth, 1997; Ng'weno *et al.*, 2019), but also in conservation conflicts because having more animals on a stakeholder's area than another can affect the equity of conservation policies (Rakotonarivo, Bell, *et al.*, 2021; Rakotonarivo, Jones, *et al.*, 2021).

Reproductive behaviour such as sexual reproduction can also be more realistically modelled with ABMs. Indeed, animals might have to actually encounter one another to reproduce, which can greatly affect population growth at low densities. Allee effects (1931) predict that a sexually reproducing population's growth rate can turn negative at low densities due to increasing difficulty to find mating partners, which greatly increases extinction probability; an effect that might be stronger in actual systems than mathematical theory predicts (Stephens and Sutherland, 1999; Berec, Angulo and Courchamp, 2007). A more mechanistic modelling of sexual reproduction can make better predictions of the impact of Allee effects on population dynamics.

Regarding decision-making modelling, switching the focus from proportion of players applying a given strategy like in GT, towards the individual choices of players according to the information they possess, allows several progresses in the simulation of stakeholders' behaviour. By having each agent make their own choice, inter-individual variability is generated. For example, in Kamra *et al.* (2018), each agent position in the forest defence game are sampled at random for the distribution generated by the neural network. In *GMSE* (Duthie *et al.*, 2018) the ABM approach is twofold. First, each land-user chooses their strategy – allocation of budget to the different actions available – independently. And second, the genetic algorithm simulating decision making is itself an ABM. It is based on the assumption that humans usually cannot scan for every single possibility to choose the optimal one but are rather good at choosing the best option that they can conceive. The genetic algorithm consists of generating a population of random strategies and letting them evolve on their own timeline according to natural selection-inspired processes (mutation, crossover, translocation) until a strategy comes out as the fittest in the population (Hamblin, 2013). In both cases, each agent chooses its own strategy, generating inter-individual variability and the strategy selection process allows for suboptimal choices. This efficiently simulates implementation uncertainty because it accounts for the fact that all agents will not always behave as expected.

1.5.3. Spatial and temporal scale

With this switch in point of view comes a change in the spatial and temporal scales of models' application. The explanatory power of ABMs will be maximised for small, countable populations while MMs are better suited to very large populations, where the averaging of inter-individual variability in the lower-level components can be safely ignored (e.g., country demographics, chemistry, fluids mechanics, etc …) (DeAngelis and Grimm, 2014). This is why the global densities switch from real numbers in MMs to integers in ABMs (Uchmański and Grimm, 1996; Grimm, 1999). Such a change of spatial scale is more adapted to conservation problems, as management is usually undertaken at the scale of a region or of a reserve and managed populations rarely exceed tens of thousands. Even more when the managed population is endangered, as population size can be reduced to only a few individuals.

In ODE systems, all life events happen at once between two timesteps, so animals are born, reproduce, are consumed, and die in proportions in a single timestep. In ABMs, the time between each individual life event can be modulated and the probabilistic approach of their realisation makes it impossible to predict which animal will do what at a given timestep, thus allowing agents to accomplish a variety of actions during their lifetime (Uchmański and Grimm, 1996). This is more in accordance with real-world systems where different life events or different decision-making sequences happen at different time of the year, and that their individual realisation is not a certainty. Allocating this time between different life events also allows for the inter-individual variability to fully express its potential on population dynamics or decision-making. Once again, this allows for a better accounting of process and implementation uncertainties.

1.5.4. Spatially explicit modelling

This leads to another key asset of ABMs: spatially explicit modelling (DeAngelis and Yurek, 2017). ABMs often feature a landscape in the shape of a lattice grid in which cells characteristics can vary. As independent entities, individuals in ABMs can have coordinates describing a position on this landscape. The rules governing the changes in these coordinates can be very diverse; from random to oriented towards the most resourceful areas (Schmitz and Booth, 1997). These rules generate spatial heterogeneity in animals' density on the landscape, thereby accounting for another aspect of process uncertainty. Similarly, resources availability can vary from one area to another, either because of an implemented stochasticity, or because resource consumption was more important on one area than another due to heterogeneity in the consumer density on the landscape. The heterogeneity in both animal density and resources availability is of key importance in ABMs because it can generate variability in the number of interactions between animals across the landscape, which is common in real-world systems and can have a strong impact on management policies efficiency but is hardly simulated by ODEs or matrix models.

Note that modelling resource heterogeneity does not necessarily requires an agent-based approach (see DeAngelis and Yurek (2017) for a review). In a model of moor land management, Chapman *et al.* (2009) modelled the landscape as a lattice grid in which each cell has a given distribution of heather and graminoid, according to which a density of sheep is computed. The distribution of vegetation cover then changes according to the level of sheep grazing and the heather burning strategy applied. This example also shows that a spatially-explicit approach allows for land-users to make decision given the situation on their own piece of land (Duthie *et al.*, 2018; Termansen *et al.*, 2019; Nilsson *et al.*, 2021), instead of based on the overall situation like in GT problems, also generating inter-agent variability in decision-making.

A spatially explicit landscape is also of great help to model monitoring techniques (Nuno, Bunnefeld and Milner-Gulland, 2013) because agents can be placed on the landscape to simulate the observation. Therefore, their estimation of the density on the landscape will depend on the actual distribution of animals in the areas where the observations have been simulated (Zurell *et al.*, 2010; Duthie *et al.*, 2018). Once again, spatial heterogeneity in animals position plays an important role here, and observation uncertainty is more accurately accounted for.

In conclusion, the spatially explicit feature of ABMs allows for a better modelling of the spatial heterogeneity in resources distribution, animals density and human decision-making and for a better accounting of the process, model, observation, and implementation uncertainty.

1.5.5. Non-equilibrium ecology

Uchmański and Grimm (1996) argued that MMs usually rely on the assumption that natural systems are inherently stable, only to be disturbed by environmental perturbations. They would be either at equilibrium or in the process of returning to equilibrium. The existence of equilibrium states (where the growth rate is persistently null) is an important assumption to solve ODE systems, but its soundness is debated in the literature (Abrams, 1980; Uchmański and Grimm, 1996; Grimm, 1999; Chesson, 2000). An interesting feature of ABMs is that this assumption is relaxed, and ABMs can be analysed regardless of the existence of equilibrium states. ABMs also acknowledge that perturbation in the system do not only come from environmental changes but also from variability in animals' interactions due to their intrinsic differences. A mechanism that should be accounted for when evaluating management strategies.

1.5.6. Critiques

It has often been said that ABMs are harder to develop, harder to communicate and harder to analyse (Uchmański and Grimm, 1996; DeAngelis and Grimm, 2014). Indeed, ABMs require more complex coding, which would makes them potentially more prone to bugs or imperfect design, which can cause distrust as programs were not communicated in research outputs (Grimm, 1999). To act on this and on the problem of model communication, the Overview, Designs and Detail protocol have been proposed (Grimm *et al.*, 2006, 2010, 2020). This is a standard protocol to communicate ABMs in research, offering different levels of details about the conception of the model. Readers with different levels in modelling can therefore get the information needed to fully understand and estimate their confidence in the model conception. The 'Details' section presents the algorithms of the sub models involved in the simulation process (the inclusion of flowcharts is encouraged) in a more precise way, allowing modelling-advanced readers to consolidate their belief in the soundness of the coding. Coupled with the recent democratisation of open-source code and public online repositories, any doubtful reader will be able to check the lines of code directly and potentially collaborate to improve it.

Another criticism is that ABMs would lack the structured methods of analysis that many mathematical models possess, such as solving methods, stability analysis, phase diagrams (Grimm, 1999). Indeed, the agent-based approach often comes with a larger number of parameters, more tipping points and more nonlinear relationships but ABMs do have their own analysis framework now, notably with adapted methods of parameter exploration, calibration and sensitivity analyses (Thiele, Kurth and Grimm, 2014; ten Broeke, van Voorn and Ligtenberg, 2016). Yet, it is fair to say that they are indeed more complex, and that the validation of an ABM requires more steps, than the usual modelling frameworks (Stillman *et al.*, 2015).

Another caveat might be the accessibility of the coding language that are optimised for ABMs. Indeed, object-oriented programming languages such as C++ require quite advance coding skills (compiled language, memory management). But ABMs coding is increasingly seen as building blocks to be connected to one another to create a given process of research interest (DeAngelis and Grimm, 2014), and simplified coding languages and platforms have been developed in that sense. For example, *NetLogo* (Wilensky, 1999) is a platform to create all sorts of ABMs from blocks and the validation process is greatly simplified thanks to a cross-platform with *R* (Thiele, 2014).

All of these challenges led to the widespread concern about researchers putting more effort into the production of the model than in the analyses (Grimm, 1999; DeAngelis and Grimm, 2014), and there is indeed an important compromise to be addressed between complexity and value of information for conservation. The different aspects of agent-based research might require more effort than other modelling approaches, therefore demanding more diverse, larger research groups to efficiently distribute skills and make sure that all the aspects of the research receive the same level of attention.

1.6.Knowledge gap and thesis outline

The previous section showed how ABMs can improve management strategy evaluation in complex conservation problems, but applications are still scarce. Besides *GMSE* and *RangeShifter*, which I have already presented from different angles, an early application was the *SIMSPAR* agent-based model of the Cape Sable seaside sparrow population dynamics. With a spatially explicit topography, this model was meant to predict the effects of water management strategies on the sparrow nesting success (DeAngelis and Grimm, 2014). Another example is *inSTREAM* (Railsback, Ayllón and Harvey, 2021), which predicts the response of trout populations downstream of hydroelectric dams to the impact of different dam management strategies on the alternative flow and temperature of the river, thus informing dams administration.

In this thesis, I take advantage of ABM assets to propose new modelling tools in the hope of improving management strategies evaluation in two complex conservation problems: the management of conservation conflicts and the management of species endangered by apparent competition.

1.6.1. Complex problem 1: Conservation conflicts

Conservation conflicts (CCs) are situations of clashing interests between conservation and human livelihood. CCs form complex socio-ecological situations where population dynamics, managers' policy making and land-users' decision making interact in various ways to impact conservation success and the social equity of conservation measures. In Chapter 2, I take advantage of the level of complexity that ABMs can simulate to question an understudied aspect of adaptive management of conservation conflicts: the timing of managers' intervention. I propose and test a new strategy for managers to time their intervention more efficiently, that I build as a new functionality in the software *GMSE*. I also present a novel method to evaluate the efficiency and social equity of different strategies and apply it to my timing strategy in a general case of CC. This example shows how to estimate if my strategy is relevant in each case and the kind of information that can be obtained from it.

1.6.2. Complex problem 2: Apparent competition

In predator-prey systems, apparent competition (AC) is an indirect negative interaction between prey species that share one or more common predators. When species involved in such indirect interactions are of conservation interest, their management can easily produce unexpected adverse effects on one another. Yet, the impact of spatial heterogeneity in resource distribution or in habitat suitability, of foraging behaviours on AC dynamics, and of how management affects them, are still poorly understood. These questions call for several assets of the ABM approach, but there are no existing ABM of apparent competition yet. In Chapter 3, I introduce and validate a novel multi-species, multi-layer, time and spatially explicit ABM of trophic interactions in which apparent competition can emerge from individual interactions. I designed the model to ease the inclusion of the mechanisms evoked earlier. In Chapter 4, I add a management option to my model, and demonstrate how it should be used to evaluate management strategies for the conservation of a species endangered by apparent competition. Through the validation and the use of my model, I confront its outcomes to the largely mathematical model-based AC theory, fleshing out how ABMs can contribute to improve our understanding of apparent competition and provide new insights for better conservation of apparent competition systems.

2. Intervene or wait? A model evaluating the timing of intervention in conservation conflicts adaptive management under uncertainty

This chapter was published in Ecology and Society, available online at this link. I led the research, programming, simulation, analysis, writing and my supervisory team – Jeroen Minderman, Nils Bunnefeld, Aileen Mill, A. Bradley Duthie – contributed.

Abstract

The timing of biodiversity managers' interventions can be critical to the success of conservation, especially in situations of conflict between conservation objectives and human livelihood, i.e., conservation conflicts. Given the uncertainty associated with complex social-ecological systems and the potentially irreversible consequences of delayed action for biodiversity and livelihoods, managers tend to simply intervene as soon as possible by precaution. However, refraining from intervening when the situation allows can be beneficial, notably by saving critical management resources. We introduce a strategy for managers to decide, based on monitoring, whether intervention is required or if waiting is possible. This study evaluates the performance of this waiting strategy compared to a strategy of unconditional intervention at every opportunity. We built an individual-based model of conservation conflict between a manager aiming to conserve an animal population and farmers aiming to maximize yield by protecting their crop from wildlife damage. We then simulated a budget-constrained adaptive management over time applying each strategy, while accounting for uncertainty around population dynamics and around decision making of managers and farmers. Our results showed that when the decision for the manager to intervene was based on a prediction of population trajectory, the waiting strategy performed at least as well as unconditional intervention while also allowing managers to save resources by avoiding unnecessary interventions. Under difficult budgetary constraints on managers, this waiting strategy ensured as high yields as unconditional intervention while significantly improving conservation outcomes by compensating managers' lack of resources with the benefits accrued over waiting periods. This suggests that waiting strategies are worth considering in conservation conflicts because they can facilitate equitable management with a more efficient use of management resources, which are often limiting in biodiversity conservation.

Résumé

Le timing d'intervention des gestionnaires de biodiversité peut être déterminant dans le succès d'un programme de conservation, tout particulièrement quand leurs objectifs sont incompatibles avec des activités humaines (conflits de conservation). Mais l'incertitude associée aux systèmes socio-écologiques, ainsi que l'irréversibilité potentielle des conséquences d'un retard d'action peut pousser les gestionnaires à simplement intervenir dès que possible. Pourtant, y renoncer quand la situation le permet peut être bénéfique, notamment en mettant efficacement à profit les ressources non-utilisées. Nous proposons ici une stratégie basée sur le monitoring pour choisir si une intervention est nécessaire ou si attendre est préférable. Cette étude évalue la capacité de cette stratégie à satisfaire à la fois les objectifs de conservation et ceux des activités humaines en comparaison avec une stratégie d'intervention systématique et inconditionnelle. Pour ce faire, nous avons développé un modèle individu-centré de conflit de conservation entre des gestionnaires cherchant à conserver une population animale et des agriculteurs cherchant à en minimiser l'impact sur leurs cultures. Nous avons ensuite simulé une gestion adaptative du conflit sous contrainte budgétaire pour chaque stratégie, tout en prenant en compte l'incertitude associée à la dynamique de la population et à la prise de décision des parties prenantes. Quand la décision était basée sur une prédiction de la trajectoire de la taille de la population, notre stratégie était au moins aussi performante qu'une intervention inconditionnelle et permettait aux gestionnaires d'économiser des ressources en évitant des interventions non nécessaires. Lorsqu'un budget trop faible rendait la gestion difficile, notre stratégie a considérablement amélioré les résultats relatifs à la conservation en compensant le manque de ressources par les bénéfices accumulés au cours des périodes sans intervention. Ces résultats montrent que notre stratégie devrait être envisagée car elle peut assurer une gestion équitable du conflit tout en permettant une utilisation plus efficace des ressources de gestion, souvent limitantes en conservation de la biodiversité.

2.1. Introduction

With an ever-growing industrial and agricultural demand in certain parts of the world, the amount of the Earth's surface used for human activities is increasingly large and often overlaps with the ranges of species of conservation concern. A conservation conflict can arise when such a species is strictly protected but also impacts human livelihood, potentially leading to a clash of interests over management decisions (Redpath *et al.*, 2013, 2015). Diverging objectives can lead land-users to defect from policies by ignoring or subverting them and engage in illegal activities often hindering conservation objectives (Bunnefeld, Hoshino and Milner-Gulland, 2011; Bainbridge, 2017; Glynatsi, Knight and Lee, 2018; Rakotonarivo *et al.*, 2021). These conflicts are especially serious when conservation and protection interferes with essential livelihood activities such as agriculture (Behr, Ozgul and Cozzi, 2017; Mason *et al.*, 2018). Conservation policies must therefore be in line with land-users' interests to ensure compliance and maximize conservation success while minimizing the impact on food security and/or farmers' income. Moreover, because conservation conflicts form complex systems with multiple biological, environmental, geographical, and social components, the response to change in these interlinked social-ecological systems is difficult to anticipate (van Wilgen and Biggs, 2011; Glynatsi, Knight and Lee, 2018; Mason *et al.*, 2018). To avoid unforeseen perturbations that might jeopardize biodiversity conservation or human livelihood, management should also embrace the uncertainty around ecological processes and human behaviour (Fryxell *et al.*, 2010; Bunnefeld, Hoshino and Milner-Gulland, 2011; Schlüter *et al.*, 2012; Cusack *et al.*, 2020).

A practical way to deal with uncertainty challenges and complex systems is adaptive management, a technique seeking to improve management iteratively by learning from its outcomes (Williams, Johnson and Wilkins, 1996; Hicks *et al.*, 2009; Keith *et al.*, 2011). It is particularly well adapted to conservation conflicts management because regular monitoring and policy updates enhance the ability to trade-off between opposing interests (Redpath *et al.*, 2013; Wam *et al.*, 2016; Mason *et al.*, 2018; Richardson *et al.*, 2020). Adaptive management thus tailors the conservation policy as closely as possible to the system's variations, but when and why to update the policy can be key to better management of social-ecological systems and conservation conflicts (Pérez, Ruiz-Herrera and San Luis, 2020). Because the consequences of mismanagement can be detrimental and even sometimes irreversible (e.g., crop losses and/or animal population extinction; Kaswamila, Russell and McGibbon (2007)), conventional wisdom might suggest that conservation success will be maximized by reacting as often as possible with updated policy. But waiting can ultimately lead to better management results when well-planned, because it can bring a variety of benefits, including enhancing knowledge through monitoring or research (Walters, 1986; Gregory, Ohlson and Arvai, 2006; Nicol *et al.*, 2019). For example, Sims and Finnoff (2013) modelled the progression of the slow and predicable spread of an invasive species and showed that, due to the knowledge acquired during the period of waiting, a delayed time of first intervention was more efficient in reducing both the spread and damages on the focal ecosystem than intervention immediately after detection of the invasion. In contrast, a delayed intervention when the invasion was fast and erratic caused a loss of control over the species progression, eventually leading to a state where any intervention became pointless. In an adaptive management context, Iacona, Possingham and Bode (2017) modelled a national parks' bird diversity protection scheme and showed that waiting and saving conservation funds to accrue interest before spending it progressively on protection achieved a higher number of protected species and a quicker recovery of the extinction debt than front-load spending. Because financial and human resources for management are often limited (Hughey, Cullen and Moran, 2003; McDonald-Madden, Baxter and Possingham, 2008), intervening when the benefits of waiting outweigh the risks can be unnecessary spending, if constraints on conservation funding allocation allows it (Wam *et al.*, 2016; Wu *et al.*, 2021). This trade-off between instances of intervention and waiting in an adaptive management process has not yet, to our knowledge, been explored in the context of conservation conflicts. We hypothesize that by refraining from intervening when conflicting stakeholder interests are already aligned, managers could save resources and use them to enhance impact when intervention will be most needed to deliver conservation and/or land-users' objectives. We predict that it is likely to be especially relevant in situations where a manager's lack of resources could be compensated for by benefits accumulated over a period of waiting.

To investigate the effect of the timing of intervention on management quality while accounting for the different sources of uncertainty associated with conservation conflicts, we used the generalized management strategy evaluation framework (*GMSE*, Duthie *et al.* (2018)). *GMSE* builds on the management strategy evaluation (MSE) framework, which aims to explore the possible outcomes of alternative management scenarios in order to assess their adequacy to managers' objectives (Smith, Sainsbury and Stevens, 1999). MSE, first developed in fisheries and later for terrestrial species, decomposes the process of natural resources adaptive management over time with sub-models of population dynamics, monitoring, management decision-making and harvesting activities, which inform and influence each other. This structure helps to isolate different components of uncertainty associated with each process when evaluating a scenario (Bunnefeld, Hoshino and Milner-Gulland, 2011). *GMSE* uses an individual-based approach for all four sub-models, simulating uncertainty intrinsically (Grimm, 1999; DeAngelis and Grimm, 2014), and includes a decision-making sub-model for manager and farmer agents that simulates goal-oriented behaviour with the possibility of sub-optimal choices. Furthermore, by generating differences between agents, individual-based models (IBMs) can model another potential source of conflict: the inequitable distribution of costs and benefits among stakeholders. Rakotonarivo *et al.* (2021a; 2021b) showed that a higher perceived equity in conservation measures among farmers increased the propensity to choose pro-conservation options. Among-user equity is thus important to model and monitor during conservation conflicts management. Knowing this, we further develop and apply *GMSE* to evaluate the efficiency of alternative management timing strategies against unconditional intervention and determine whether and how a profitable timing trade-off can be found for conservation conflict management under uncertainty.

We modelled a budget-constrained adaptive management of a conservation conflict in which a wildlife animal population of conservation concern negatively impacts agricultural activities, and farmers can respond by culling to minimize yield loss. We propose two novel timing strategies for the manager to determine whether the situation warrants intervention when the resources saved by waiting generate long term benefits. Through simulations with *GMSE*, we assessed how each timing strategy affected the quality of management regarding the conflict between biodiversity conservation and agricultural production objectives. We thereby determined for which conditions our alternative strategies resulted in better management than intervening at every opportunity.

2.2.Methods

2.2.1. Model overview

2.2.1.1. Model case

To simulate conservation conflict management over time, we develop an individual-based model with a population of wildlife animals (referred to as 'population'), farmers, and a manager all interacting on an agricultural landscape. The landscape is divided into discrete cells, each of which produces an agricultural yield and can hold any number of animals. Each farmer owns a contiguous block of cells that forms their 'land', and the sum of its cells' productivity determines the farmer's yield. Animals consume agricultural resources from landscape cells to survive and reproduce, which consequently reduces the farmers' yield. Farmers can cull animals that are on their own land to reduce yield loss. The manager attempts to avoid extinction by maintaining the population around a predefined target size (T_N), as previously done in, e.g., the management of conflict between mountain nyala antelope conservation and trophy hunting in Ethiopia (Bunnefeld, Hoshino and Milner-Gulland, 2011), or between farming and migrating birds' protection in Scotland or Sweden (Bainbridge, 2017; Mason *et al.*, 2018; Nilsson *et al.*, 2021). This target was chosen to be high enough to prevent extinction, but low enough to ensure a satisfactory yield to farmers. The manager's method is to implement a policy incentivizing or disincentivizing culling as appropriate to get the population size closer to T_N. Hence, following an adaptive management process, the manager updates this policy according to the monitoring of the population size (N_t) at each timestep t.

2.2.1.2. Manager policymaking

The manager receives a fixed, non-cumulative budget B_M at the beginning of each timestep, which we interpret to reflect the total time, energy, or money available to the manager to implement a change of policy and enforce culling restrictions. The policy is modelled as a cost that farmers must pay to cull an animal on their land. The manager can draw into B_M to raise this cost to discourage farmers from culling and favour population growth and can decrease it to facilitate culling and favour a population decrease. To model the budget needed to enforce a restricting policy, every increase of 1 in the culling cost requires an investment of 10 b.u. from the manager. Conversely, as the manager does not need to incentivize farmers to remove animals when the policy allows high culling rates, they do not need to spend budget to decrease the cost. The amount by which the manager changes the culling cost is computed by *GMSE*'s evolutionary algorithm according to their goal that was modelled as minimizing the distance between N_t and T_N.

2.2.1.3. Timing strategies

We explored three timing strategies that determine whether a manager intervenes and updates the policy or waits and leaves it as is. The Control strategy (CTL) was the null model in this study. It corresponds to unconditional intervention at every opportunity and was modelled as the manager updating the policy at every timestep. With the Adaptive Timing of Intervention strategy (ATI), we define a permissive range P_T around T_N in the form of $T_N \pm P_T$. Within this range, the manager considers N_t close enough to T_N, and consequently, that the current policy results in a sustainable culling rate for the population. Hence, the manager will update the policy if and only if the population is monitored outside $T_N \pm P_T$. The Trajectory (TRJ) strategy is the same as the ATI strategy, except that when N_t is inside $T_N \pm P_T$, the manager makes a prediction on next timestep's population size in the form of a linear extrapolation based on the current and preceding monitoring results. If this prediction falls inside $T_N \pm P_T$, the manager leaves the policy unchanged; otherwise, they update it. In both ATI and TRJ strategies, after a timestep without updating the policy, the manager receives an additional proportion B_b of their initial budget to model the benefits associated with waiting. This bonus can be accumulated over several consecutive timesteps of waiting but is lost as soon as the manager draws into their budget to raise the level of restrictions again (modelling details in Appendix A1).

2.2.1.4. Farmers action planning

At the beginning of each timestep, each farmer receives a fixed, non-cumulative budget B_F, which they allocate to culling a certain number of animals on the land that they own at the cost set by the manager's policy. A minimum cost of 10 b.u. models the baseline budget needed for a farmer to cull an animal. The number of animals culled is independently computed for each farmer using *GMSE*'s evolutionary algorithm, meaning that each farmer makes an independent decision for how to act according to their goal: maximizing their own yield.

2.2.2. Simulations with *GMSE*

To simulate conservation conflict adaptive management with different timing strategies under uncertainty, we used the R package '*GMSE*' (Duthie *et al.*, 2018). See Appendix A1 for further details on modelling, parameter choices and simulations.

2.2.2.1. Initial parameters

We modelled the landscape as a grid of 40 equally sized rectangular pieces of land, each individually owned by a farmer. We model a population that is stable in absence of culling, but under the threat of extinction for a high culling rate. We defined the population dynamics model parameters such that population density stabilised quickly and steadily. The farmers were provided with an initial budget high enough to cull up to the expected number of animals on their land when the population is at equilibrium (B_F = 1000 b.u), so the population went extinct if the conflict was left unmanaged. At first, the manager's initial budget was set equal to the farmers' one (B_M = B_F = 1000 b.u) and manager's target was set at half the equilibrium size (T_N = 2000 animals). The initial population size was set at N_0 = 1000 animals, which is sufficiently low for the population to be under immediate threat of extinction and justify the initial involvement of a manager. We chose these parameters for the Control strategy to produce adequate management while also leaving room for improvement and determine the extent to which alternative strategies can generate better results.

2.2.2.2. Population dynamics sub-model

GMSE's population dynamics model features a population of N animals, each of which has an age and a position on the landscape. In each timestep, each animal moves from its current cell to a random cell within a defined range. Upon arrival, the animal consumes a proportion of 0.5 of the cell's remaining yield. All animals move 12 times during a single timestep in a random order. After all movement and feeding, animals asexually produce one offspring for every 5 resource units consumed, which are added to the population as new individuals. Next, animals that have consumed over 4.75 resource units and have an age ≤ 5 timesteps survive, the others are removed from the population. This consumption criteria leads to density-dependent intra-specific competition for resources, and modelling life events discretely generates inter-individual variability, as well as geographical and demographic stochasticity, therefore accounting for several sources of uncertainty around population dynamics.

2.2.2.3. Monitoring sub-model

We assumed that the manager makes no errors during monitoring, thus N_t represents the exact population size at each timestep. This assumption avoided modelled stochastic monitoring errors that would have challenged a full understanding of management dynamics.

2.2.2.4. Decision-making sub-model

In each timestep, manager and farmer decision-making are independently modelled using evolutionary algorithms, allowing the emergence of a conflict when agents' goals are opposed. This approach computes practical but not necessarily optimal decisions, recognizing that most people cannot think of every single possibility to choose the optimal one, but can choose the best option among those they could conceive (Hamblin, 2013; Duthie *et al.*, 2018 [SI1]), generating uncertainty around stakeholders' individual decision-making.

2.2.3. Experimental plan

2.2.3.1. Systematic parameter exploration

To assess management quality of ATI and TRJ in terms of population dynamics and farmers yield, we varied the permissiveness P_T and budget bonus B_b across a range of values for each strategy and compared the outcomes with those of CTL. P_T ranged from 0% of the manager's target T_N (unconditional update at every timestep, i.e., CTL) to 100% of T_N (update only in the extreme situations where the population is extinct or close to natural equilibrium size) by 10% increments. B_b ranged from 0% of the manager's initial budget B_M (no bonus following a timestep of waiting) to 100% of B_M by 10% increments. For each unique combination of P_T and B_b, we ran 100 independent simulation replicates of management over a period of 20 timesteps under identical initial conditions.

2.2.3.2. Management outcomes

We defined the most desirable outcomes as when management prevents the population from going extinct (1), while keeping it as close as possible to target (2) and ensuring the highest yield to farmers (3) with the lowest inequity among them (4). For a particular combination of parameters, extinction risk (1) was assessed as the frequency of extinction events over all replicates, denoted f_{ext}. We measured how close to target the population was (2) with the difference between the population size (N_t) and the manager's target (T_N) weighted by T_N at the end of a simulation averaged over all replicates, denoted d_T, in % of T_N. Farmers' total yield (3) was calculated as the ratio of the sum of all cell's yield at the end of a simulation over the maximum yield the landscape can provide in the absence of animal consumption (40000 yield units) averaged over all replicates and denoted Y_{end} in % of the landscape's maximum productivity. The among-farmer inequity (4) was measured as the difference between the lowest and highest farmer's yields weighted by the highest yield at the end of a simulation, averaged over all replicates, denoted Y_{ineq}, in % of the highest yield. Finally, we computed the proportion of timesteps without manager's intervention over the time length of a simulation and averaged it over all replicates, denoted t_w ($1-t_w$ is thus the proportion of policy updates). We computed 95% bootstrapped confidence interval around each average (Manly 2007). The equity between stakeholder groups was assessed by systematically confronting the conservation and the agricultural outcomes to detect unbalanced repartition of costs and benefits.

2.2.3.3. Sensitivity to manager's budget

We hypothesized that the effect of the budget bonus amount (B_b) on management quality would be stronger in situations of higher budget constraint on the manager. To test for this, we selected the permissiveness of 50%, in which outcomes with TRJ were not different from CTL but with a weak B_b effect (see section 2.3.2). We decreased the manager's initial budget (B_M) from 1000 to 500 b.u. by 100 b.u. increments. For each B_M, we varied B_b from 0 to 100% of B_M by 10% increments in 100 replicates, and measured the same outcome proxies as the previous section to investigate the effect of B_b amount on management quality according to B_M. We also simulated management with CTL for each B_M value to check how well the waiting strategies performed in comparison. This sums up to 60 different combinations of B_M and B_b, for an additional 6000 independent simulations.

2.3. Results

2.3.1. Adaptive Timing of Intervention strategy

2.3.1.1. Conservation outcome

When applying the Adaptive Timing of Intervention (ATI) strategy, increasing the permissiveness value caused the extinction risk to increase, and the final population size to decrease below target with no marked effect of the budget bonus B_b (Figure 1 and A2.1). No combination of permissiveness and bonus amount resulted in equivalent or lower extinction risk than CTL strategy ($f_{ext} = 0.15$ with [0.08 ; 0.22] 95% confidence interval). No parameter combination of ATI strategy resulted in the population being closer nor equally close to target as CTL strategy ($d_T = -24.90\%$ [-33.78 ; -16.26]) either, which is not surprising given that extinction was almost certain for most combinations ($f_{ext} > 0.9$ for $P_T > 20\%$).

2.3.1.2. Agricultural outcome

Increasing permissiveness caused the farmers' final yield to increase, and among-farmer yield inequity to decrease with no effect of the budget bonus amount (Figures A2.2 and A2.3). Farmers' final yield was >90% of the maximum for all ATI parameter combinations, which was slightly more than CTL ($Y_{end} = 89.64\%$ [88.04 ; 90.90]). The among-farmer inequity was slightly lower than CTL results ($Y_{ineq} = 5.68\%$ [4.97 ; 6.34]). Indeed, as permissiveness increased, there were fewer animals feeding on farmers' land so the impact on yield was lower, and the farmers' yield got closer to maximum. Also, the highest yields attained the maximum value while the lowest kept increasing, which reduced inequity.

2.3.1.3. Mechanisms underlying the outcomes

With ATI, most extinction events occurred when the population was monitored to exceed the permissive range, and in response, the manager lowered the level of culling restrictions to favour population decrease down to target. A problem arose when, in the following timestep, the population was monitored inside the permissive range because it caused the manager to leave the policy unchanged. Farmers then continued to cull at a low cost, driving the population to extinction at the next timestep (Figure 2, ATI panel). Consequently, the larger the permissive range around target, the more likely this was to happen, thereby explaining why the extinction frequency and deviation from target increased with permissiveness values. This misinterpretation from the manager regularly occurred in the ATI parameter areas with very high extinction frequency (Figure 1), in which the population deviation from target at the timestep preceding extinction was within the manager's permissive range (Fig. A2.4). Hence, the most effective strategy for avoiding population extinction here was to intervene unconditionally in every timestep, at the expense of slightly decreasing farmers' final yield.

2.3.2. Trajectory strategy

2.3.2.1. Conservation outcome

When applying TRJ, the extinction frequency and deviation from target were at least as close to 0 as CTL for permissiveness values up to 80%, without the manager intervening up to 40% of the time (Figure 1, A3.1 and A3.2). The budget bonus value had either no effect or a weak effect on the outcomes. Several combinations resulted in an extinction frequency under 0.1, even 0 sometimes, while f_{ext} = 0.15 [0.08 ; 0.22] with CTL. The effect of bonus amount was slightly stronger in the 40 and 50% permissiveness range (Fig. A3.2), where bonus values between 20 and 50% resulted in the population being closer to target than CTL (d_T = -24.90% [-33,78 ; -16.26]). We chose the 50% parameter area for the experiment on sensitivity to manager's initial budget to test whether this weak effect could amplify when applying stronger budget constraints on the manager.

2.3.2.2. Agricultural outcome

With TRJ, the farmers' final yield was as close to maximum, and the among-farmer yield inequity was similarly low as the CTL strategy regardless of the permissiveness and budget bonus value (Figures A3.3 and A3.4).

2.3.2.3. Mechanisms underlying the outcomes

The rare extinction events with CTL seem to have occurred when population was over target and the manager decreased the level of restrictions by too much, or when farmers happened to cull more than expected, which caused the population to decrease beyond reparation (Figure 2, CTL panel). TRJ strategy may have avoided this imprecision by offering managers the possibility not to intervene at these moments where the population is in the upper permissive range and keep the population closer to target (Figure 2, TRJ panel). The absence of effect from the budget bonus amount was most likely caused by the manager initial budget alone often being enough to efficiently ensure both population maintenance and farmers' yield given our initial parameter values, leaving no room for improvement due to a bonus. Thus, TRJ achieved similarly good management outcomes to CTL without managers having to intervene at every timestep, and regardless of the amount of benefit obtained from waiting periods.

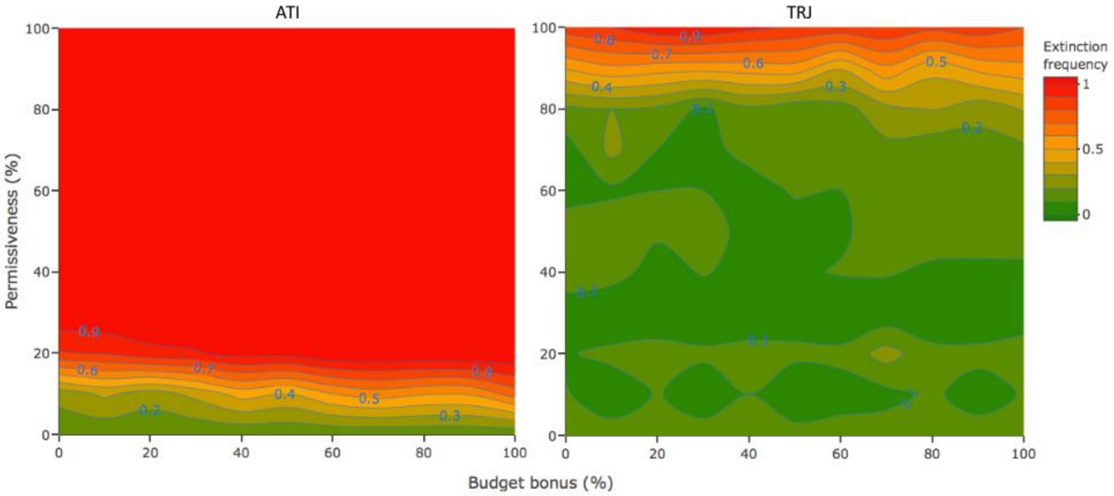

Figure 1. Extinction frequency (f_{ext}) according to the permissiveness (P_T) and budget bonus (B_b) combinations in an individual-based model simulating the management of a population under conditions of conservation conflict. The greener, the lower the risk of extinction. The band formed by $P_T = 0$ and the corresponding B_b values are the f_{ext} obtained with the control strategy (CTL). With adaptive timing of intervention strategy (ATI; left panel), there was no combination of P_T and B_b parameters resulting in as low a f_{ext} as control strategy (CTL; 0.15 [0.08; 0.22] 95% CI), and population extinction was almost certain in most cases, with a weak positive effect of B_b regardless of the permissive range size. With the trajectory strategy (TRJ; right panel), most areas are as green as or greener than CTL's f_{ext} value, meaning TRJ performed at least as well as CTL regarding extinction risk. The effect of B_b on f_{ext} was weak to absent.

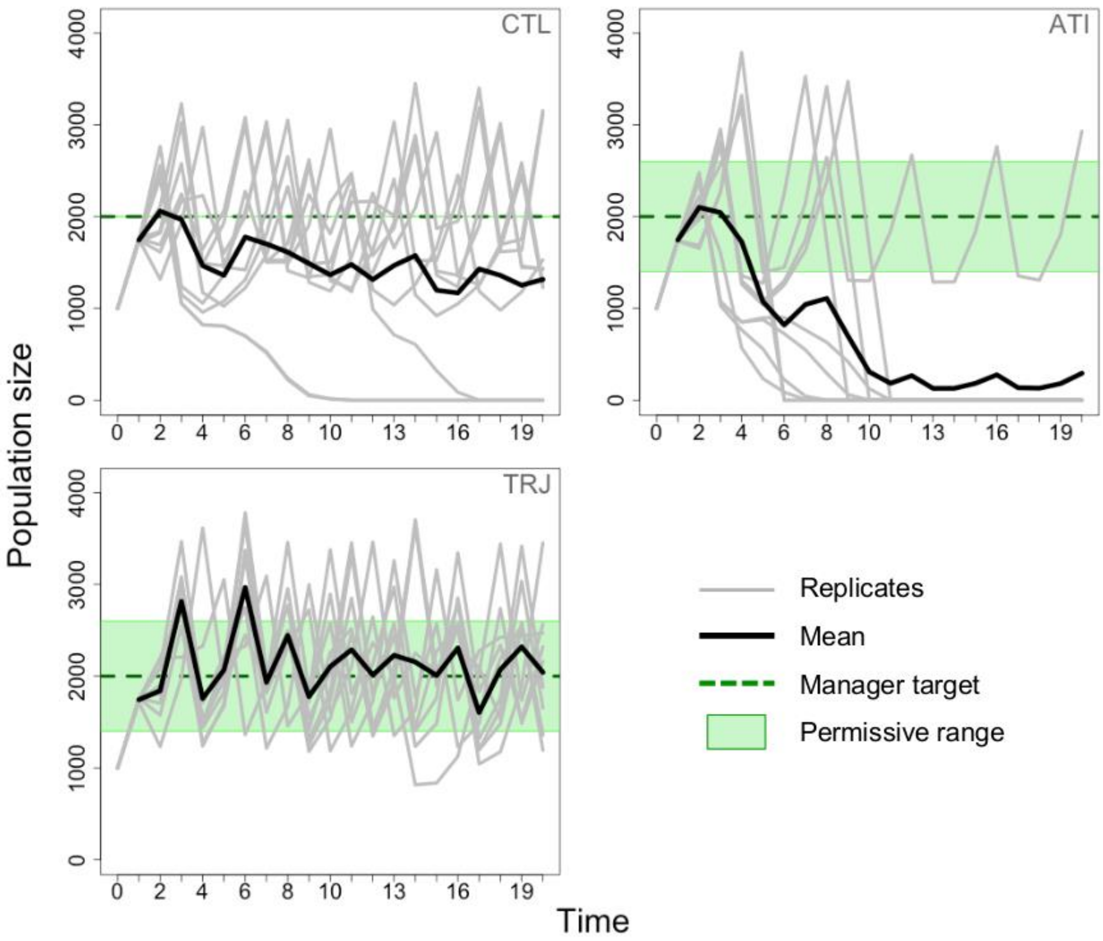

Figure 2. Average population size over time of 10 simulation replicates with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. Upper left: manager intervenes unconditionally (control strategy, CTL). Extinctions happened when the population got too far below target size (T_N) between two consecutive timesteps for the manager to be able to rectify by increasing restrictions. Upper right: manager applies the adaptive timing of intervention strategy (ATI; permissiveness (P_T) = 30%, Budget bonus (B_b) = 10%). Most extinctions happened when population size was over the permissive range, then was monitored into it the following timestep. Thus, the manager did not update the policy, allowing farmers to continue culling at a low cost, frequently driving the population to extinction at the following timestep. Note: in the replicate that did not result in extinction, the population was never monitored into the permissive range during a decrease, causing the manager to update the costs and control the situation with better timing. Lower left: manager applies the trajectory strategy (TRJ; T_N = 30%, B_b = 0%). The TRJ strategy avoided some extinction events.

2.3.3. Sensitivity to manager's initial budget

2.3.3.1. Conservation outcome

The extinction frequency increased, and the final population size decreased below target, with decreasing the manager's initial budget (Figure 3). But for B_M = 800 b.u., the extinction frequency steadily decreased from 0.71 [0.61 ; 0.80] without budget bonus to 0.07 [0.02 ; 0.12] for a bonus of 30% of B_M (Figure 3), which is significantly closer to zero than CTL for the same initial budget (f_{ext} = 0.76 [0.67 ; 0.83]). At higher bonuses, the extinction frequency increased again between 0.3-0.6, which is lower than CTL, although still a high extinction risk. The same trend was observed in the distance to target, which rose from −78.4% of T_N [-84.9 ; -70.9] without budget bonus, to −11.4% [-21.4 ; -2.1] for the same bonus of 30% of B_M (Figure A4.1); CTL being −83.7% [-88.7 ; -78.0] (Figure A4.1).

2.3.3.2. Agricultural outcome

The farmers' final yield increased, and the among-farmer inequity decreased with decreasing manager's initial budget (B_M) because of the positive effect on extinction risk and the negative effect on population size (Figures A4.3 and A4.4). In the B_M = 800 b.u. area, the farmers' final yield was between 85% and 100% (for the highest extinction frequency) without varying markedly with the bonus amount. With the bonus of 30% that critically improved conservation outcomes, the final yield was 89.20% [87.47 ; 90.76] instead of 97.18% [96.14 ; 99] with the CTL strategy for the same manager's budget (at the expense of a very high extinction risk). The inequity was 5.94% [5.23 ; 6.68] instead of 2.11% [1.65 ; 2.6] with CTL, which is still relatively low.

2.3.3.3. Mechanisms underlying the outcomes

For the manager's initial budget value that maximized the budget bonus' negative effect on extinction risk and positive effect on population size (B_M = 800 b.u.), if the manager intervened at every timestep or used TRJ but without getting any benefit from the waiting periods, extinctions occurred when the population fell to too low a population size. It was then challenging for the manager to rectify the population trajectory with only their initial budget as the culling cost was always too low to efficiently reduce farmers' culling rate (Figure 4, CTL). If, in this situation, the manager accumulated budget bonus from previous waiting period(s), they had enough power to enforce higher restrictions on farmers as soon as the population did, or was predicted to, fall under the manager's permissive range. Intermediate bonus amounts ensured that, when the latter happened, the population could increase closer to the manager's target (Figure 4, TRJ). TRJ thus appeared to be more efficient than CTL in situations of stronger budget constraint on the manager. In such situations, the role of the budget bonus was critical in decreasing the extinction risk, while maintaining a high and equitable yield to farmers and allowing the manager to save 20 to 30% of their interventions (Figure A4.2).

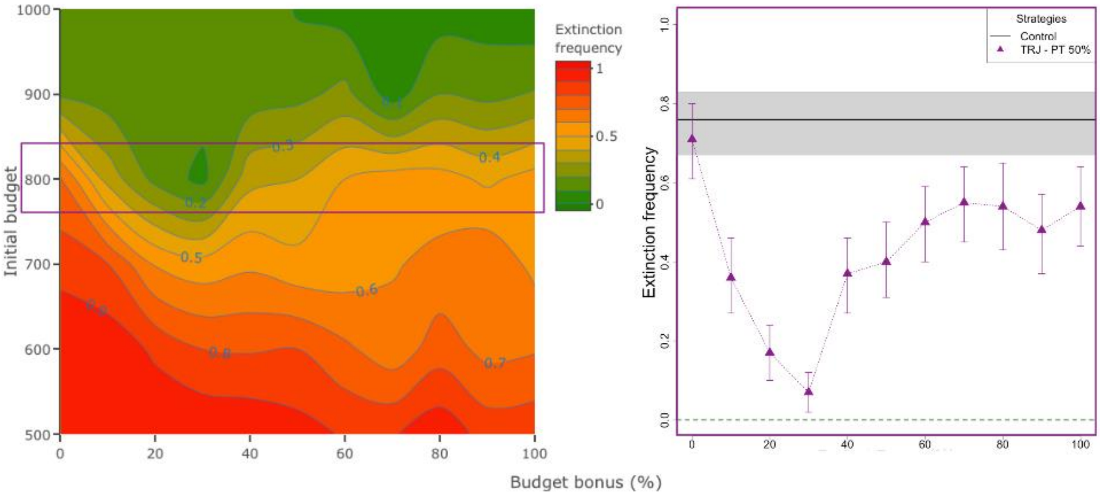

Figure 3. Extinction frequency when applying the trajectory strategy (TRJ); permissiveness (P_T) = 50%, according to manager's initial budget (B_M) and budget bonus amount (B_b) in an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the lower the extinction frequency. For B_M = 800 b.u. (violet square, detail on the right panel), a pit forms along increasing B_b values, meaning that low to intermediate values for B_b markedly lowered the extinction risk. Error bars show 95% bootstrapped confidence intervals. The black line is the f_{ext} with control strategy for the same initial budget and the grey shaded area the 95% confidence interval around it.

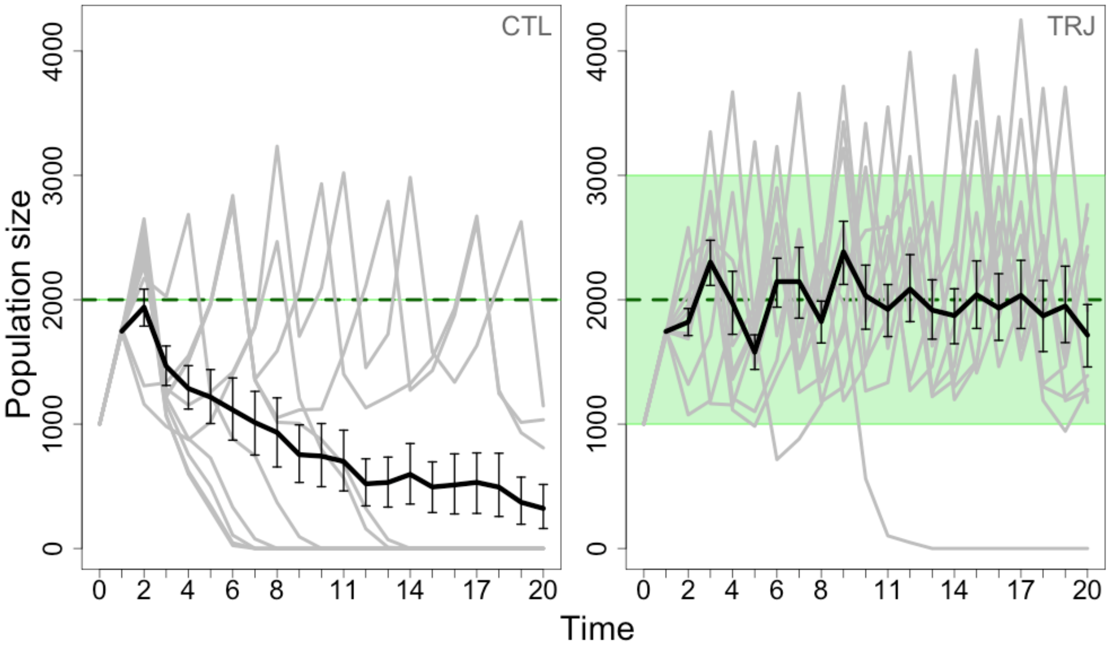

Figure 4. Population size over time averaged over 50 replicates (thick black line, error bars being the 95% confidence intervals) plotted on 10 replicates (thin grey lines) with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict and an initial budget of 800 b.u. The green dotted line shows manager's target (T_N), and the green area represents the permissive range $T_N \pm P_T$. Left panel: manager applies the control strategy (CTL). Extinctions happened when the population got too far below the manager's target (green dotted line) between two consecutive timesteps for the manager to be able to rectify with their initial budget only. Right panel: manager applies the trajectory strategy (TRJ; P_T = 50%, B_b = 30%). Thanks to the benefits accumulated over waiting periods, the manager was able to raise the culling cost high enough to maintain farmers' culling rate at a sustainable value. The replicate that resulted in extinction was caused by a strong misprediction of timestep 10's population size, causing the manager to wait while intervention was needed.

2.4. Discussion

2.4.1. Summary of the study

When adaptively managing a conservation conflict in a social-ecological system, our modelling of strategies dynamically alternating between intervention and waiting found that management outcomes were better when the decision to intervene was made based on a prediction of the system's response than when based on the latest monitoring results alone. With prediction-based decisions, conservation and agricultural outcomes were at least as good as intervening unconditionally, while allowing the manager to save management resources and avoid unnecessary, potentially harmful interventions. When a low budget limited a manager's ability to effectively manage the conservation conflict, the benefits accrued during waiting periods were applied when intervention was most critical and greatly improved conservation outcomes with only a weak impact on farmers' yields and equity. Naturally, the main risk with waiting strategies is to decide to wait when intervention is needed, or to intervene when waiting is preferable. Basing intervention only on current monitoring should be avoided because when population density is monitored inside the permissive range during a sharp increase or decrease, managers can mistakenly conclude that the policy is adequate when, in fact, keeping the same policy running again can lead to extinction or critical yield loss. Basing intervention on population trajectory instead also includes a risk of inaccurately predicting the population density to be within the permissive range, encouraging the managers to wait while the policy is inadequate to align conservation and agricultural objectives. Nevertheless, the consequences for yield loss or population decline were reversible when using an adequate permissive range.

2.4.2. Importance of budget and monitoring in waiting strategy's efficiency

The superiority of our Trajectory strategy over unconditional intervention depended on the manager's budget. When the budget was high enough to manage the situation efficiently with the Control strategy, the outcomes with the Trajectory strategy were at least as good as unconditional updates regardless of the budget bonus amount. This suggests that interventions when the population was monitored within the permissive range and predicted to stay in it (i.e., oscillating close to target) were less useful. Since the initial budget was sufficient for satisfactory management, the benefits reaped during waiting periods with the Trajectory strategy could not further improve the management outcomes. This is relevant because human, financial and time resources are limited in conservation and there is a constant competition for their allocation to cases (Hughey, Cullen and Moran, 2003; McDonald-Madden, Baxter and Possingham, 2008; Jachowski and Kesler, 2009; Ruiz-Miranda, Vilchis and Swaisgood, 2020). It is also increasingly recognized that different species can impact human livelihood in different ways and at different times within the same geographical area, which should be considered in management (Pozo *et al.*, 2021a, 2021b). Intervention in one conflict could thus be a priority for a time, and then deprioritized when another requires intervention more urgently. Therefore, resources unused during periods of waiting in a well-funded case could instead be allocated to other, potentially less well-funded and/or more pressing cases and improve overall conservation benefits (Wu *et al.*, 2021). Our Trajectory strategy can thus help a dynamic allocation of management resources to cases that need them the most at a given instance.

When a limited budget made management more challenging, the resources saved when not intervening using the Trajectory strategy could generate enough benefits to compensate for the lack of resources. We emphasize that the prediction based on population trajectory is a means for managers to reduce the risk of misjudging the timing of intervention; what improved management here was better access to the benefits accumulated over waiting periods. This result supports previous modelling results in Iacona, Possingham and Bode (2017), where national park managers did not have enough budget to put every endangered bird species under protection at once but could maximize success by waiting and saving their funds to gradually enhance their monetary power. Importantly, this is only possible if unused management resources are not revoked or reallocated when less needed. A review of exit-strategies in conservation by Ruiz-Miranda, Vilchis and Swaisgood (2020) shows that withdrawing funds when objectives are attained is very uncommon in adaptive management (but should be more considered and carefully planned). The present study suggests that the budget saved during waiting periods should be reallocated if the management resources are not limiting but invested in improving future interventions if they are.

To isolate the effect of various timing strategies on management quality, we assumed that the manager had perfect knowledge of population size. But real-world monitoring involves uncertainty that plays an important role in the success of conservation (Bunnefeld, Hoshino and Milner-Gulland, 2011; Nuno, Bunnefeld and Milner-Gulland, 2013). Monitoring uncertainty will cause errors in estimating population density, and therefore errors in deciding if the situation requires intervention. This will decrease the efficiency of both unconditional intervention and Trajectory strategies, but the latter might be more impacted because errors will influence both monitoring and trajectory prediction, therefore mitigating the advantage over unconditional intervention. Indeed, the efficacy of Trajectory strategy might rely on more regular and accurate monitoring, which might not always be possible or affordable. Testing the effect of observation accuracy or cost on management quality is beyond the scope of this study, but it is an important aspect to consider when applying timing strategies (McDonald-Madden, Baxter and Possingham, 2008; Milner-Gulland, 2011; Wu *et al.*, 2021).

Since our focus is on management strategy and not on control measures, we limited farmers' options to culling for the sake of simplicity and ease of model interpretation. We did not model indirect measures such as fencing, widespread in the management of conservation conflicts over land-use (Nyhus, 2016; Pooley *et al.*, 2017), as these measures are rather permanent constructions that are not always fitted to the regular changes and updates of our adaptive management process. Nevertheless, future modelling might usefully consider a range of alternative options for population management.

2.4.3. Modelling novelties for adaptive management

The ongoing 6th mass extinction under a rapidly changing climate (Ceballos, Ehrlich and Dirzo, 2017) and the consequences of land-use conflicts between agriculture and wildlife protection on food security often put conservation managers under urgency (Du Toit, 2010). Our results suggest that the urgency to act should not mean systematic, unconditional intervention and stress the importance of acquiring information to choose wisely how and when to intervene. As with software such as *ISIS-fish* (Mahévas and Pelletier, 2004) or *FLR* (Kell *et al.*, 2007) in fisheries management, the method developed here can inform managers' policymaking. Parameterizing *GMSE* with empirical data from a conflict between farming and common cranes in Sweden has previously permitted the evaluation of subsidy levels that best balanced culling and scaring for the maintain of both population and farmers' income (Nilsson *et al.*, 2021). Likewise, targeted parameterization of our model can give managers information to decide how permissive they should be and how much gain they should expect from waiting periods for our strategy to be useful regarding conservation, land-users' objectives, and management resources allocation efficiency.

The individual-based nature of our model and the modularity of the *GMSE* framework accounts for several sources of uncertainty around population dynamics and stakeholders' individual decision making. Our mechanistic model simulates population dynamics with intrinsic demographical uncertainty (inter-individual variability in the realization of life events) and geographical uncertainty (animals' movement is stochastic; Uchmański and Grimm (1996), Stillman *et al.* (2015)). Future work could also include explicit modelling of environmental uncertainty, potentially in the form of stochastic extreme events impacting both population dynamics and farmers' yields. Currently, our results are robust even if population dynamics are uncertain and if spatial distribution can induce inequity by having the animals sometimes being more numerous on one farmer's land than another. Yet, Rakotonarivo *et al.* (2021a; 2021b) showed that the perceived equity in the balance of costs and benefits of conservation actions between and among stakeholders' groups plays an important role in land-users' propensity to choose pro-conservation strategies. However, the aspect of equity in conservation conflicts has scarcely been incorporated in modelling results. For example, Wam *et al.* (2016) used a measure of monetary equity between different stakeholder groups in their management model balancing logging, livestock grazing and game hunting activities in a boreal forest. Our method also controls between-stakeholder equity by systematically confronting the population dynamics and the farmers' yield. In addition, we used a new indicator for among-stakeholder equity by measuring the success of our strategies against the difference between the lowest and highest farmers' yields. Among-stakeholder equity, to our knowledge, has not been modelled before in conservation conflicts, and modelling stakeholders individually like the present study offers a direct measure of equity among members of the same group, thus allowing its monitoring as an important outcome of management.

The lack of dynamic stakeholder behaviour modelling has been identified as a major cause of failure in conservation (Schlüter *et al.*, 2012). Previous studies have addressed this by modelling decision-making using game theory (Colyvan, Justus and Regan, 2011; Glynatsi, Knight and Lee, 2018). Nevertheless, a game-theoretic framework can have limitations when applied to management decision-making, including fixed behaviour rules, finite sets of actions (e.g., cooperate or defect) and the assumption that players are perfectly rational and aware of the best options for them (Myerson, 1991). In this model, we use evolutionary algorithms, a form of artificial intelligence, for managers and farmers to make decisions, which we show here offers a heuristic to find practical solutions when the panel of options is too large for game theoretic problems (Hamblin, 2013). We combined the evolutionary algorithms with an individual-based approach and model decision-making independently for each stakeholder with the possibility for sub-optimal choices along a continuum of possible actions (see also Kamra *et al.* (2018), Cusack *et al.* (2020), Nilsson *et al.* (2021)). Simulating these different sources of uncertainty in our experiments allowed to conclude that the strategy we proposed is relevant even if managers do not always make the most efficient policies and if farmers do not always behave as they were expected to.

2.5.Conclusion

We use an uncertainty-robust modelling tool to compare the management quality of waiting strategies against unconditional intervention regarding conservation and agricultural objectives and discuss which strategy to prefer according to cases of conservation conflicts. We propose a strategy for managers to dynamically alternate between intervening and waiting informed by population monitoring. When the decision to intervene or wait is based on a prediction of population trajectory, our strategy can result in a better, more equitable management of conservation conflicts, especially in situations of limiting budget. By saving time, energy and/or money when intervention is not necessary, it can also ensure a more efficient use of management resources.

3. Introducing an agent-based model for apparent competition systems' management

Abstract

Apparent competition is an indirect negative interaction between prey species mediated by a shared predator. Its intensity varies with asymmetry in predation, prey characteristics, or spatial-temporal structure. Species of conservation interest are often involved in such interactions, which complicates predictions of indirect consequences of management on other species in the system. This is especially true when conservation measures impact spatial heterogeneity in resource distribution or habitat suitability, and when managed species have structured life cycles or exhibit complex individual behaviours. Agent-based modelling approaches handle such complexities especially well but, to date, management strategy evaluation in apparent competition systems have used classical mathematical models. In this chapter, I introduce a spatially explicit multi-species, multi-layer agent-based model of trophic interactions in which apparent competition can emerge, integrating the aforementioned mechanisms simultaneously with a better simulation of uncertainty. I validate the model in its essential version with a sensitivity analysis by measuring the strength of apparent competition when varying different sources of asymmetry. My model was particularly sensitive to asymmetry in preys' resource availability, prey resource consumption, and prey quality for predators. It was less sensitive to asymmetry in preys' catch probability and fertility. Overall, the model behaves as theory and empirical cases predict, with some interesting exceptions that challenge results from mathematical models. Notably, apparent competition intensified with increasing asymmetry in preys' resource availability, which was not predicted by the usual P* rule, indicating the need for more careful consideration of management measures influencing this factor (e.g., supplementary feeding) than existing theory advises. Also, the emergent shapes of predator's functional and numerical responses differed from the usual shapes in mathematical models. By relaxing this key assumption, ABMs can simulate particular cases more accurately and, therefore, better inform managers. My results also showed that, unlike theory predicts, oscillations in population densities might not necessarily induce weaker apparent competition. These results enrich understanding of apparent competition and underscore the utility of the agent-based framework for addressing complex conservation challenges. My model is fit for purpose and ready to integrate more complex spatial structures and individual behaviours.

Résumé

La compétition apparente est une interaction négative indirecte entre une ou plusieurs espèces proies par le biais d’un prédateur commun. Son intensité varie en fonction de l'asymétrie dans la prédation, dans les caractéristiques intrinsèques des proies ou de la structure spatio-temporelle. Des espèces préservées sont souvent impliquées dans ce type d’interaction, ce qui complique l’anticipation des conséquences indirectes des programmes de conservation sur les autres espèces du système. Particulièrement lorsque ces programmes impactent l'hétérogénéité de la distribution des ressources ou de l'habitat, et lorsque les espèces concernées ont des cycles de vie complexes ou présentent des comportements particuliers. L’approche individu-centrée gère particulièrement bien cette complexité mais, jusqu'à présent, l'évaluation des stratégies de gestion dans les systèmes de compétition apparente utilise des modèles mathématiques plus classiques. Dans ce chapitre, je présente le premier modèle de compétition apparente individu-centré, qui peut intégrer les mécanismes susmentionnés tout en permettant une meilleure simulation de l'incertitude associée. Je valide le modèle dans sa version la plus essentielle via une analyse de sensibilité mesurant l’intensité de la compétition apparente en réponse aux variations des différentes sources d'asymétrie. Mon modèle est particulièrement sensible à l'asymétrie dans la disponibilité des ressources des proies, dans le niveau de consommation de ressources des proies et dans la qualité des proies pour les prédateurs. Il était moins sensible à l'asymétrie dans la probabilité de capture et la fertilité des proies. Dans l'ensemble, le modèle se comporte comme attendu par la théorie et les études empiriques, à quelques exceptions intéressantes près qui remettent en question les prédictions des modèles mathématiques usuels. Notamment en ce qui concerne l'impact de la disponibilité des ressources, de l'amplitude des cycles et de l'absence d'hypothèse sur la réponse fonctionnelle du prédateur, sur l'issue de la compétition apparente. Mon modèle est maintenant prêt à incorporer des structures spatiales et des comportements individuels plus complexes.

3.1.Introduction

3.1.1. Definition

In population dynamics, apparent competition (AC) is an indirect negative interaction between individuals, populations, species, or entire functional groups, mediated through the action of one or more species of shared natural enemies (Holt, 1977; Holt and Bonsall, 2017). More specifically, in predator-prey systems, AC is an indirect interaction between several prey species mediated by a shared predator. A perturbation in species dynamics or behaviour can thus have an impact on the other species through the change induced in predation pressure. For example, following a particularly mild winter in North America, a great increase in the population densities of deer and moose in caribou foraging range led to a higher density of predator, which resulted in a concerning decline in the caribou population (Serrouya *et al.*, 2015). Thus, even if there is no direct competition for resources, an increase in moose and deer densities can still have a negative impact on Caribous density mediated by predation. Because conservation can directly impact a population’s dynamics, indirect effects of population changes on other species are important for predicting the consequences of management strategies. I introduce an agent-based model simulating apparent competition in trophic systems to help anticipate these consequences and inform decision making in conservation policies.

3.1.2. Drivers

First, where does AC come from? In a review of theoretical and empirical studies of AC, DeCesare *et al.* (2010) suggest that two species having a shared predator (or predation niche overlap) is sufficient for a system to exhibit apparent competition, and asymmetric predation is often added as another necessary condition (Wittmer, Sinclair and McLellan, 2005; Holt and Bonsall, 2017). If predation is symmetric in absence of competition for resources, apparent competition is at its lowest level because both preys undergo predation to the same extent. Both prey species should stabilise at lower densities in the presence of the other prey species than they would be in the absence of the other prey species, but this negative predation-mediated effect is the same for both preys (Holt, 1977; Bonsall and Hassell, 1997). Asymmetry in predation would induce a difference in the strength of this negative effect according to the prey species.

Asymmetric predation can come from predators exhibiting different behaviours towards different preys. The predator must first be capable of feeding on multiple prey species (DeCesare *et al.*, 2010) and have different functional response (relationship between catch rate and prey density) and numerical response (relationship between prey and predator densities) that differ according to prey species (Wittmer *et al.*, 2013; Barraquand *et al.*, 2015). For example, different handling time (time and energy spent capturing, consuming, and digesting a catch) between preys can impact apparent competition outcomes. The prey that has a longer handling time will keep predator occupied and satiated for longer (lower catch rate, weaker functional response), relieving predation on other preys, but a prey that has a shorter handling (higher catch rate, stronger functional response) will leave more time for predation on the other preys. This is illustrated in Sundararaj *et al.* (2012), in which they hypothesised that populations of local endangered ungulates could benefit from a predation relief because lions spent more time handling catches from livestock prey populations.

Differences between prey in resource exploitation efficiency, fertility, and the ability to withstand predation are other potential sources of asymmetric predation (Holt, 1977). Indeed, in situations of apparent competition, generalist predators often subsist on an abundant primary prey species that has high fitness to predation, but occasionally feed on a less abundant, less predation-resistant, secondary prey species (Sinclair *et al.*, 1998). An example can be found in Roemer, Donlan and Courchamp (2002), in which the proliferation of introduced feral pigs on an island, which had a high fertility rate and vulnerability to predation, increased the density of golden eagles and consequently intensified predation on endemic foxes, which were less abundant and less fertile than feral pigs.

Another source of asymmetry in predation can come from the spatial features of the trophic system. For example, the reduction of suitable habitat drove moose to forage on caribou wolf hunting area, which subsequently increased wolf numbers and predation on protected caribous (Wittmer, Sinclair and McLellan, 2005). Environmental patchiness can lead to apparent competition between prey species (Bonsall and Hassell, 1997). Indeed, if either prey species gets spatially clustered in a shared patch and attracts predators, there might be a negative impact on the other prey species locally, but also a predation relief at a global scale because of the predators' aggregation around one patch. Another example is refuge-mediated apparent competition, in which a landscape feature, or a species, provides something attractive to another species (e.g., shelter, shade, humidity) that intensifies consumption or predation on other species locally (Orrock, Holt and Baskett, 2010). An interesting example was studied by Mouquet *et al.* (2005) in a case of plant-mediated apparent competition between ant colonies and one of their parasites. The presence of a particular plant species of gentian provides refuge from predation to the parasite larvae, making contact between parasites and ants more likely, which therefore increases the negative effect on ant colonies.

There are other sources of apparent competition, such as the so-called mesopredator release effect; an increase in predation by intermediate predators when removing an apex predator. Courchamp, Langlais and Sugihara (1999), showed that, in an island community that includes birds and rodents with a shared cat predator, a sudden removal of cats would be extremely detrimental for birds because the rodent population has a much higher growth rate than the birds, which would greatly increase rodent predation on them in absence of rodent control by cats. Another source can be a time lag in a predators' response to a decline in prey densities, which temporarily maintains a high density of predators over a low density of preys (Serrouya *et al.*, 2015). Thus, the spatial or temporal features of the system can also have a strong impact on the outcomes of AC (Holt and Lawton, 1993; Morris, Lewis and Godfray, 2005; Wittmer, Sinclair and McLellan, 2005; Oliver, Luque-Larena and Lambin, 2009; DeAngelis and Yurek, 2017). Any combination of all the aforementioned sources, and of course, any human intervention that would impact them, could potentially severely influence the intensity of AC in the system. This is why spatial and temporal dimensions must be taken into account alongside the more typically studied characteristics of the animal populations to anticipate the consequences of apparent competition following the implementation of a conservation policy.

I identified the asymmetry in prey species growth rates, carrying capacities, predator functional and numerical response as the intrinsic drivers for asymmetrical apparent competition.

3.1.3. Detection

The way AC is measured, and the indicators of AC, vary a lot in the literature but are mostly based on the fluctuations in population densities following the perturbation of a predator - prey system. The change in predator density is referred to as the AC response, and the relative change in preys' densities that follows is the AC effect (Abrams, 1998; Hart, Freckleton and Levine, 2018). For Holt (1977), if there is a shared predator in a system, the densities of prey populations are lower in the presence than they are in absence of the other prey, and the competitor that experiences less AC is the one that can both sustain and withstand the highest number of predators when at equilibrium, or the 'P* rule' (Holt, Grover and Tilman, 1994). More precisely, the winning prey is expected to be the one with the highest growth-rate-to-attack-rate ratio. Besides, Serrouya *et al.* (2015) applied an ODE model to a population of caribou impacted by predator-mediated apparent competition and notably showed that an increase in the carrying capacity of the primary prey resulted in a lower equilibrium density of the secondary prey. In a review of the role of apparent competition in conservation, DeCesare *et al.* (2010) also identified asymmetry in relative attack rates as evidence of apparent competition; that is, the number of predator attacks on one prey were lower in absence than in presence of other preys. This review also mention a decrease in the relative fitness of prey following a perturbation (Chesson and Kuang, 2008), as well as shifts in predator functional response as potential markers of AC. Predators can exhibit a switch from regulatory predation to depensatory predation of the secondary prey (citing Forrester and Steele (2004)). Most of the time in AC, the primary prey will exhibit regulatory predation while the secondary prey will exhibit depensatory predation (Sinclair *et al.*, 1998).

In a case particularly relevant to conservation, Ng'weno *et al.* (2019) demonstrate that a concerning decrease in hartebeest population density was caused by apparent competition with zebras mediated by lions. The study showed on site that (i) zebras were lions' primary prey, as they were most often consumed by lions with only a weak effect on zebra population's growth rate. (ii) Hartebeest exhibited a predator mediated Allee effect, because in presence of a predator population, hartebeest growth rate became negative at low densities. (iii) Hartebeest were preferably selected by lions when present (negative Jacob index of selectivity, Jacobs (1974)). There was a predation niche overlap demonstrated by (iv) a higher hartebeest mortality zones with high concentration of zebra and (v) a hartebeest survival twice as high in zones where fewer zebras occurred.

To measure AC intensity, it might be possible to use preys' interspecific competition coefficients, as in Lotka-Volterra competitive equations of preys competing for resources (Abrams, 1980). But initial explorations suggest that such coefficients are less well adapted for situations where competition is mediated by predation. Indeed, this approach would require a prey intraspecific competition coefficient that includes the negative effect of predation on the prey's growth rate in absence of other preys. In other words, the per-capita effect of a prey on the prey population growth rate would be decomposed into a coefficient of intra specific competition for resources and a coefficient for intra specific competition through the sustaining of the predator population. First, it would imply a fixed and known numerical response from the predator. Second, that the competition coefficients are constant regardless of the presence, absence and density of other preys (which is true under very specific assumptions seldom verifying in nature; Abrams (1980)). Even if these assumptions were safe to make, the intensity of AC is only linked to the change in predator population density, so if prey species do not compete for resources, then the inter specific competition coefficient between preys will most likely be null anyways because all the AC effect will be attributable to the change in predator density. Similarly, preliminary exploration ruled out the mutual invasion criterion as a measure of AC, which is less suited to study across-trophic-levels coexistence, systems with important Allee effect and more largely to predator-prey systems. Moreover, the impact of demographic stochasticity on the invasion criterion is still an open question (Chesson, 2000; Grainger, Levine and Gilbert, 2019). Consequently, I identified the densities, the catch rates, and the extinction rates, before and after the perturbation, as the important variables to follow to inform decision making in conservation of AC systems.

3.1.4. Importance for conservation

Conservation measures and/or biodiversity management can induce a rapid change in the dynamics and behaviours of species within a trophic community. Intervention on one species of conservation interest can thus indirectly impact other species in the food chain through predation, unexpectedly increasing the density of a population that managers or land-users want to be low or decrease the density of a population that they want to be high. The human-mediated introduction of a previously absent species, either by accident (e.g., the introduction of ship rats on islands), for human livelihood (e.g., cats for rodent control; Courchamp, Langlais and Sugihara (1999)), or for conservation purposes (e.g., reintroduction of golden eagle on islands; Roemer *et al.* (2001); Roemer, Donlan and Courchamp (2002); Courchamp, Woodroffe and Roemer (2003)) perturbs the population dynamics over a very short time window (see DeCesare *et al.* (2010) for a comprehensive review). A classic case is the introduction of rabbits on islands that are intended for human consumption, which subsequently increase the population size of introduced cats that intensify total predation on local endangered birds species (Courchamp, Langlais and Sugihara, 2000).

Unexpected consequences of apparent competition can also lead to conservation conflicts. A good example is human management of the game hunted red grouse in the UK, which is predated upon by hen harriers (Thirgood *et al.*, 2000; Redpath and Thirgood, 2009). Because the raptor is protected by The Wildlife and Countryside Act 1981, grouse keepers are not allowed to use destructive methods to prevent hen harrier predation on grouse, so some have introduced diversionary prey (voles). But it caused the total density of hen harriers to increase, thereby having the opposite effect and ultimately intensifying predation on grouse. This unintended consequence of diversionary prey introduction led grouse keepers to use destructive control methods on hen harriers, resulting in a conservation conflict between raptor conservationists and game keepers and hunters. More complex modelling that incorporates apparent competition could potentially anticipate such conflicts and help in their avoidance or mitigation.

3.1.5. Modelling

To better predict the unintended indirect consequences of species dynamics under apparent competition and ultimately avoid mismanagement, the use of population dynamics models to simulate conservation scenarios *in silico* is an important tool for improving decision-making. Most models use a system of ordinary differential equations (ODE) to model apparent competition, with each ODE describing the change of a species' density. The most common ODE systems are derived from the Lotka-Volterra (LV) population model (Holt, 1977; Holt, Grover and Tilman, 1994; Courchamp, Langlais and Sugihara, 1999, 2000; Roemer, Donlan and Courchamp, 2002; Courchamp, Woodroffe and Roemer, 2003), and less often from MacArthur-Rosenzweig's population model, a derivation of the LV population model better integrating indirect interactions (Serrouya *et al.*, 2015). Some studies use models such as Leslie's matrices (Mouquet *et al.*, 2005), coupled-lattice model (CML, in which several patches can inform each other in terms of inputs for their internal mathematical model; Bonsall and Hassell, (2000)). Beside this variety of mathematical, deterministic models (which outcome is always the same with a given parameter set), agent-based approaches remain under used.

Although uncertainty is increasingly recognized as a key aspect for conservation and biodiversity management (Bunnefeld, Hoshino and Milner-Gulland, 2011; Keith *et al.*, 2011; Nicol *et al.*, 2019), deterministic models are less adapted to simulate uncertainty (Uchmański and Grimm, 1996; DeAngelis and Grimm, 2014). Indeed, models are expected to inform on which aspect of the system needs research, how to dimension monitoring, knowing the room for manoeuvres and margin of error (Williams, Johnson and Wilkins, 1996; Nuno, Bunnefeld and Milner-Gulland, 2013). Examples of studies incorporating uncertainty in apparent competition dynamics are rare, but Roemer, Donlan and Courchamp (2002) did assess uncertainty around their modelling results by varying their parameter values by a few percents and estimated the impact on their focal species density at the end of simulation. Conservation in AC systems could thus benefit from a modelling framework that better integrate uncertainty.

3.1.6. Knowledge gaps

The review on apparent competition by Holt and Bonsall (2017) identified several open questions in apparent competition theory. Specifically, the effect of spatial heterogeneity on the outcomes of apparent competition is of primary interest, and a limited number of studies have explored some aspect of it (Morris, Lewis and Godfray, 2005). For example, Bonsall and Hassell (2000) used a coupled lattice model of dispersal to investigate the effect of environment patchiness on AC. The investigation of the impact of more complex population structures on apparent competition dynamics is also still in progress. For example, different age classes and the time spent in each developmental stage can influence the outcomes of AC (Bonsall and Hassell, 1997). Mouquet *et al.* (2005) demonstrated the effect of population structure on AC using an age structured Leslie matrices model. Foraging behaviours are also expected to greatly impact AC, as explored by Courchamp, Langlais and Sugihara (1999), Roemer, Donlan and Courchamp (2002), Courchamp, Woodroffe and Roemer (2003) with a Lotka-Volterra model that simulated predator preferences through biases in predator's diet and prey catch rates. It is also increasingly recognised that the existence of equilibrium states in populations dynamics are dependent on very specific assumptions (Abrams, Holt and Roth, 1998), which are seldom verified in the field (DeAngelis and Grimm, 2014; Stillman *et al.*, 2015). Indeed, temporal variability such as seasonality or different phenology, as shown in Holt and Barfield (2003) or Smith and Hall (2016) with models coupling Lotka-Volterra equations and time series analysis, can greatly impact the assumption of equilibrium. All these avenues for progress in AC theory could benefit from a more flexible and versatile modelling framework.

3.1.7. Relevance of agent-based approach

Although much theoretical progress concerning apparent competition has been made using mathematical models and the diversity of their respective assets, the assumptions of these models can also limit the kinds of theoretical inferences that can be made. Agent-based models (ABMs) provide an alternative, more flexible framework to incorporate multiple complex features of biological systems. Indeed, mathematical models are perhaps better suited to general, large-scale questions where the impact of specific and local complexities can be safely ignored. Nevertheless, apparent competition conservation problems are most likely to have a specific and local focus (e.g., with implications at the scale of a region, a reserve, or a protected area), are often spatially explicit by nature (e.g., land-use change, connectivity changes or refuge-mediated AC), and unexpected responses often stem from local interactions between animals and between animals and their environment. The bottom-up approach of agent-based modelling is therefore theoretically more appropriate for addressing questions at this scale (Schmitz & Booth 1997), as finite and small populations, non-equilibrium dynamics, and flexibility in individual behaviours are amongst the key advantages of agent-based modelling (Uchmański and Grimm, 1996; DeAngelis and Grimm, 2014; Stillman *et al.*, 2015). Moreover, for very large food webs, ODE systems stability analysis can become very complicated, perhaps even intractable. In contrast, ABMs can more easily handle a large number of different populations.

Despite that, the agent-based approach is not widespread in conservation, even if it has been demonstrated to be very useful in ecology (Stillman *et al.*, 2015). For example, The *Gecko* agent-based framework (Schmitz and Booth, 1997) showed the importance of active foraging behaviour on the persistence of a tuft-grasshopper-spider trophic system. The *MORPH* model (Stillman, 2008) can predict the consequences of environmental change on foraging populations, and its *fish-MORPH* adaptation to salmonids to predict their responses to loss of flow in rivers according to dam management policies (Phang et al. 2016). *RangeShifter 2.0* (Bocedi *et al.*, 2014, 2021) is one of the most versatile examples of agent-based models used in conservation. It simulates a species' population dynamics and dispersal on a changing, spatially explicit landscape over time, and the parameters governing movement, reproduction, survival, settlement, and dispersal are changing according to evolutionary processes. *RangeShifter* was used to evaluate alternative strategies in a large diversity of biodiversity management in cases including improving landscape connectivity, species reintroduction, or the spread of invasive species. Yet, there is, to my knowledge, no existing ABM simulating apparent competition in predator-prey dynamics, nor the management of such cases.

I introduce an agent-based model of trophic interaction between primary resources, herbivores, and predators in which apparent competition can happen as an emergent feature. In this model, animals occur on a spatially explicit landscape on which resources distribution can be heterogeneous and/or exhibit patterns, animals can have different age classes, different foraging rules, and different phenology. I believe it can be an interesting virtual lab to explore the influence of these characteristics (and their combinations) on trophic systems, especially to test management scenarios and inform decision making in biodiversity conservation. This chapter presents the details of the model in its most basic version, testing its outcomes against apparent competition theory and exploring the relative impacts of the parameters underlying the rules of trophic interactions.

3.2.Model

The model description follows the ODD (Overview, Design concepts, Details) protocol (Grimm et al., 2006, 2010, 2020).

3.2.1. Overview

3.2.1.1. Purpose

The purpose of the model is to simulate the trophic interactions between several populations of primary producers, primary consumers, and predators to predict the emergence and intensity of apparent competition for research and conservation purposes. The ABM approach makes it possible for this model to account for important aspects of population dynamics that cannot be included simultaneously in deterministic models, such as spatial heterogeneity, complex population structures, complex individual behaviours, intrinsic uncertainty, or non-equilibrium dynamics. This work aims to present the details of this model in its simplest version with two prey populations using different resources and a predator population feeding on both prey species. Along with the model's calibration and sensitivity analysis, the outcomes will be compared to AC theory as a proof of concept.

3.2.1.2. Entities, state variables and scales

Landscape

All animals are simulated on a square grid lattice landscape of size S x S cells. Each cell is characterised by an x and a y location, a reference number unique to the cell, a certain amount of resources of two different kinds present on the cell, a maximum amount of resources that the cell can hold, the density of each animal present, and the counts of catches of each prey types during a timestep.

Animals

Animals move and interact on the landscape and with resources and other animals on landscape cells. They are characterised by an x and y position on the grid, a type (here prey 1, prey 2 and predator), a dead or alive status, an age, a resource stock, and a number of offspring produced. The movement range (in fraction of S), satiation level, resource cost for maintenance and for reproduction (all in resource units), diet, fertility or average expected number of offspring produced during reproduction trial, and time of introduction depend on the population they belong to. For coding purposes, each animal population is attributed a specific tag of 3 digits. Resource type tag first digit is a 1, 2 for prey, 3 for predators, and the two other digits are a number for the population (up to 99). E.g., prey 2 type tag is 202.

Animals – preys

Prey entities are modelled as a specific type of animal, distinct in the way that they harvest resources directly from the landscape cells. Each prey population have specific values for their animal characteristics and feed on its own resource (no competition for resources between prey populations).

Animals – predators

Predators are modelled as a specific type of animal entities, distinct in the way they acquire resources from capturing preys. They have additional characteristics that distinguish them from other animal entities. These characteristics are a conversion rate of a catch into resources for each prey type, and a probability of catch for each prey type. Predators feed on both prey species.

3.2.1.3. Spatial and temporal scales

Timesteps and spatial scale are abstract in the model, but in this study, a single timestep could be conceptualised as the equivalent of a month and a single grid cell could be conceptualised as equivalent to one square hectare.

3.2.1.4. Process overview and scheduling

In all the following processes involving animals in a timestep, prey populations act first, in order of tags, followed by the predator population, provided that the current timestep is passed their respective introduction time. A timestep begins with animals moving, which updates the position of each animal on the landscape and of each animal type's densities on the cells. Next, preys feed and predators hunt, which updates the animals' individual resource stock, preys' status (dead or alive) and prey type's densities on cells. With a defined frequency, the following processes occur: animals undergo a survival trial to update their dead or alive status; survivors undergo the reproduction trial to update the animals' number of offspring produced. The animal tables are updated, accounting deaths, increasing survivors age by 1, introducing offspring as new individuals and resetting offspring counters to zero. Lastly, the animal type's density is updated accordingly at the end of the timestep. A timestep then finishes by saving the density of resources, preys, catches and predators on the landscape at this instant (as a new line of a results table), before saving a spatial snapshot of the cells' information. Finally, the densities and catch counts of each animal population in the landscape table are reset to 0 to start the next timestep anew. At a defined frequency, the landscape cells resources are replenished to their maximum.

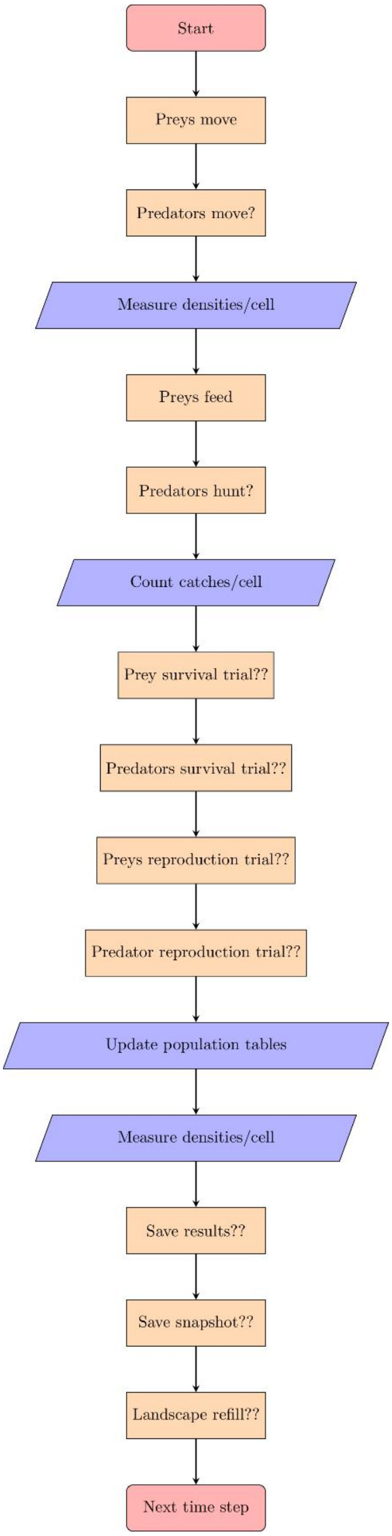

Figure 5. General flowchart of a timestep in the model. Boxes finishing with a '?' are realised only if the timestep is superior to the time of introduction of the given species. Boxes finishing with a '??' are realised only if, in addition, the timestep is a multiple of f_{surv}.

3.2.2. Design concepts

3.2.2.1. Basic principles

The model tracks the dynamics of two prey populations and one predator population involved in trophic relationship according to their interactions with a spatially explicit landscape. The two prey populations subsist on distinct resources, and there are no direct interactions between prey species. Therefore, the only source of inter specific competition between prey populations is apparent competition mediated by the predator.

3.2.2.2. Emergence

Non-emergent processes

The way landscape resources on which prey feed are replenished to their maximum (after a sequence of moving, feeding, survival and reproduction trials) at a given frequency is imposed and independent of the animals' characteristics. The number of resources that predators gain from a catch of a prey type is fixed.

Emergent features

The emergent result of the model are the population densities on the landscape. They emerge from each animal's position and resource stock, which depends on their characteristics (movement, feeding, survival, reproduction), on their interaction rules and on their relative position on the landscape. By extension, the predator's functional response (change in predator catch rate following a change in prey density) and numerical response (change in predator density following a change in prey density) also emerges from the animals' individual behaviour.

3.2.2.3. Objectives

There are no adaptive traits or evolutionary objectives in this version of the model. Feeding is modelled as an automated, unmotivated process and conditions reproduction and survival. It means that a prey automatically feeds on the cell it landed after the random moving sequence and is not drawn to a cell by any mechanism. Idem for predators that hunts preys that happen to be on the cell it landed after the random moving sequence and is not drawn to a cell by any mechanism. The question here strictly ecological and the focus is population dynamics at spatial, temporal scales, end effective population sizes too small for evolutionary processes to be relevant.

3.2.2.4. Interactions

The focus is on trophic interactions: prey directly consume resources from the landscape, and predator get resources by consuming prey. Prey's resources are made distinct to make sure that the only interactions between prey populations are mediated by their shared enemy. The diets and preferences of each population are specified in a separate table (Table 1). If an animal has a diet composed of several species, an order of preference can be specified in the table (1, 2, 3 etc).

Table 1. Structure of a diet table in the model. The values shown here were the one used in the simulations.

		“Consumes”				
		Resource type 1	Resource type 2	Prey type 1	Prey type 2	Predator
“Is consumed by”	Resource type 1	0	0	1	0	0
	Resource type 2	0	0	0	1	0
	Prey type 1	0	0	0	0	1
	Prey type 2	0	0	0	0	2
	Predator	0	0	0	0	0

3.2.2.5. Stochasticity

Movement

Animal initial positions on the landscape are generated at random by drawing their coordinates from a uniform distribution between 0 and the side size S of the landscape. When moving, an animal’s next position is computed by adding to its current x and y position two values drawn from a uniform distribution between minus and plus its movement range in x and y directions. It accounts for the fact that animal movement is hardly predictable and can be impeded or inhibited by factors that are not yet simulated in this model. Plus, Brownian motion is the least assumption in most ABMs (Bocedi *et al.*, 2014; Duthie *et al.*, 2018).

Feeding

The amount of resources taken from a cell by a feeding prey is drawn from a uniform distribution between 0 and the prey’s satiation level. It accounts for the fact that foraging efficiency depends on many other factors that are not simulated in this model. Preys feed in random order to avoid the same preys always feeding first.

Hunting

In this study, the predators are generalist, with no prey species preference simulated. Available preys on the cell the predator is located are randomized for each hunting predator to model a random first seen, first hunted behaviour. Predators hunt in random order to avoid the same predator always hunting first. Predators successfully catch a prey with a certain probability (according to prey's type). The trial is made by drawing a number from a uniform distribution between 0 and 1, and if this number is lesser than the catch probability, the catch is effective. It models the variability in preys' ability to escape and/or in predator's hunting efficiency. If the catch is successful (details in section 3.2.3.2), predator take in a fixed amount of resources according to the prey's population characteristics, assuming that they consume the whole prey caught.

It was not the case in this work, but this amount can also be drawn from a uniform distribution between 0 and the prey's max resources per catch to generate more stochasticity. It could simulate predators that do not consume their catch entirely, by behaviour or because of disturbances (scavengers, enemy approaching, kleptoparasitism, etc…) (Krofel and Jerina, 2016) or that the quality of the catch varies for reasons not explicitly modelled here.

Survival

Survival is probabilistic and dependent upon the animal's resource stock size, or the amount of resources it has accumulated between two consecutive survival trials. By default, if the animal has less resources in stock than the maintenance cost, its survival probability is 0; otherwise, it is 1. The trial is made by drawing a number from a uniform distribution between 0 and 1.

It was not the case in this work but the relationship between survival probability and resource stock size can be set to continuous, smoother functions, including linear, negative exponential, positive exponential and logistic.

Reproduction

Reproduction is asexual, probabilistic, and dependent upon the animal's resource stock size. By default, if the animal has less resources in stock than the reproduction cost, it reproduces with a probability of 0; otherwise with a probability of 1. The trial is made by drawing a number from a uniform distribution between 0 and 1; if this number is less than the reproduction probability, the animal reproduces at this timestep. The number of offspring generated is drawn from a Poisson distribution parameterized on the animals' population average offspring number (fertility). It simulates the variability in animals' clutch sizes within their population.

It was not the case in this work but the relationship between reproduction probability and resource stock size can be set to continuous, smoother functions, including linear, negative exponential, positive exponential and logistic.

Observation

The observed variables are the density of each population on the landscape and the number of successful predators catches in each prey population. In this study, these variables are measured assuming no monitoring error, after each survival and reproduction trial but the frequency of observation can be set independently. For this study, the focus is on global population dynamics, but these variables are spatially explicit and measured on each cell. They make it possible to compute other measures such as population growth rate, catch rate, extinction rate (over several replicate simulations), and intensity of apparent competition.

3.2.3. Details

3.2.3.1. Initialisation

At initialisation, two tables to store simulation results are independently constructed, one containing the characteristics of each cell (a snapshot of the landscape) and the other containing animal population densities and catch count. Resources are set to their respective maximum on each cell and animals' positions are distributed at random with an empty resource stock, alive status, 0 offspring and age 0. Timestep 0 is for setting up the structures; the life events processes start on the next timestep. Each population can have a different time of introduction: for a given population, the processes will only take place once the number of simulated timesteps have exceeded this value.

3.2.3.2. Sub models

Animals' movement

For each animal in the population table, a value drawn from a discrete uniform distribution between plus and minus the animal's movement range is added to their current x and y values before applying a correction for reflective boundaries. (If new coordinate > S, subtract S; if < 0, add S). The movement range is implemented as a fraction of the landscape size.

Animals' survival trial

For each animal in the population table, if its status is 'alive', a survival probability is computed. By default, this probability is conditional: if the animal's resource stock contains more than its maintenance cost, its survival probability is 1 and 0 otherwise. A value is then drawn from a uniform distribution between 0 and 1. If it is under the survival probability, the animal survives to the next timestep and the maintenance cost is subtracted from its resource stock (Figure 7).

Animals' reproduction trial

For each animal in the population table, if its status is 'alive', a reproduction probability is computed. By default, this probability is conditional: if the animal's resource stock contains more than its reproduction cost, its reproduction probability is 1 and 0 otherwise. If reproduction is successful, the number of offspring produced is drawn from a Poisson distribution with a rate parameter that is the animal's population fertility. That way, some animals might end up not reproducing even if they have the resources for it, simulating the possibility of unsuccessful mating, miscarriage, or external causes preventing reproduction. If the offspring number is greater than 0, the reproduction cost is subtracted from the animal's resource stock (Figure 8).

Functions linking resource pool and survival/reproduction probability

It was not used in this study, but to give a chance to animals that could not get enough resources to meet the maintenance (reproduction) cost to pass the trials, as well as making survival (reproduction) less certain when meeting the cost, I implemented several other, smoother functions for the relationship between an animal's resource pool and its survival (reproduction) probability. These smoother functions could also model the uncertainty and context dependence of different environmental conditions, e.g., climate/seasons, which might cause variation in the amount of resources required to survive (reproduce). I wanted the probability to get closer to 1 when the animal's resources exceeded the maintenance cost *mc* and closer to certain death when the animal had few resources. I set a minimal survival probability of 0.1 when the animal had 0 resources in stock (p_0), and a survival probability of 0.9 when the animal had reached exactly the maintenance cost (p_{mc}). I tested several functions positive and increasing on R+ and able to plateau at a value of 1 (Figure 6).

Exponential negative

$$p(x) = 1 - b * \; e^{-a*x}$$

With x = animal's resource stock.

Solving for $p(x = 0)$ we get $p_0 = 1 - b$ or $b = 1 - p_0$.

Solving for $p(x = mc)$ we get $p_{mc} = 1 - b * e^{-a*mc}$ or $a = -\frac{\ln\left(\frac{1-p_{mc}}{b}\right)}{mc}$.

Linear on [0 ; mc] – exponential negative on]mc ; +∞[

$$p(x) = a\,x + b$$

With x in [0 ; mc].

Solving for $p(x=0)$, we get $p_0 = b$.

Solving for $p(x=mc)$, we get $p_{mc} = a * mc + b$ or $a = \frac{p_{mc} - b}{mc}$.

Exponential positive on [0 ; mc] - exponential negative on]mc ; +∞[

$$p(x) = b * e^{a*x}$$

With x in [0 ; mc].

Solving for $p(x=0)$ we get $p_0 = b$.

Solving for $p(x=mc)$ we get $p_{mc} = b * e^{a*mc}$ or $a = \frac{\ln\left(\frac{p_{mc}}{b}\right)}{mc}$.

Logistic

$$p(x) = \frac{1}{1 + e^{-a(x-b)}}$$

Solving for $p(x=0)$ we get $p_0 = \frac{1}{1+e^{a*b}}$ or $a * b = \ln\left(\frac{1}{p_0} - 1\right)$.

Solving for $p(x=mc)$ we get $p_{mc} = \frac{1}{1+e^{-a(mc-b)}}$ or $a = \frac{1}{mc}\left(a * b - \ln\left(\frac{1}{p_{mc}} - 1\right)\right)$

Replacing $a * b$, $a = \frac{1}{mc}\left(\ln\left(\frac{1}{p_0} - 1\right) - \ln\left(\frac{1}{p_{mc}} - 1\right)\right)$.

And finally, $b = \frac{1}{a}\ln\left(\frac{1}{p_0} - 1\right)$

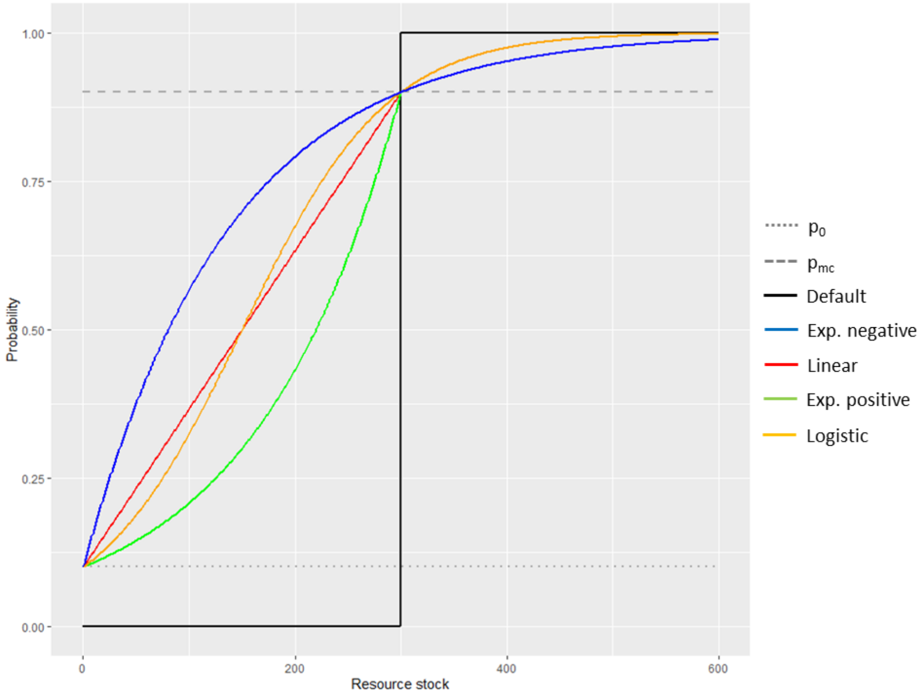

Figure 6. Different functions linking the survival or reproduction probabilities with the resource stock size of an animal. p_0 = 0.1, p_{mc} = 0.9, maintenance cost = 300 resource units.

Preys' feeding

At the start of prey feeding, a vector containing the preys' row indexes in their population table is created and shuffled to avoid having the same animals systematically feeding first. Then, for each prey in the table following the order of the shuffled indexes, the amount of resources available on the cell it is standing on is obtained by correspondence with the landscape table, and the prey transfers resources from the cell to its resource stock. If there are enough resources on the cell to match the prey's maximal consumption, the amount of resources taken is drawn from a uniform distribution between 0 and prey's maximal consumption; otherwise, it is between 0 and what is left on the cell (Figure 9). This models that resources might be harder to find when scarce and/or that most herbivores are usually able to modulate their intake according to resource availability.

Predators' hunting

At the start of predator hunting, a vector containing the predators' row indexes in their population table is created and shuffled to avoid having the same animals systematically feeding first. Then, the number and type of prey present on the cell is obtained by correspondence with the landscape table. A vector containing each prey present on the cell coded by its type (prey 1 or 2) is constructed, and the order of the prey depends on the predator's behaviour. In this study, the predator is generalist so the preys' position in the vector is shuffled randomly without bias. If there are prey present on the cell and the predator has not yet reached its satiation level, the predator parses the preys' vector, and a catching trial is realised for each prey. A number is drawn from a uniform distribution between 0 and 1, and if this number is lower than the focal prey type's catch probability, the catch is successful. The predator then gains the resources corresponding to this prey type's conversion rate in its resource stock, and the catch count and density of this prey type on this cell is updated (Figure 10).

If the predator has a strong preference for one of the prey types, the available prey vector is ranked by order of preference (Table 1). If the predator always hunts the best prey present, the available preys' vector is ranked by descending order of resources per catch.

Animals' population table update

After the survival and reproduction trials, all animal population tables are updated. A new table, of row dimension equal to the current population size plus the total number of offspring produced and subtracted the number of deaths, is constructed. Parsing the old population table, the characteristics of the animals with status "alive" are copied into the new table, their offspring number is reset to 0 and their age is incremented. If this individual reproduced during this timestep, then the corresponding number of offspring are added as new individuals (0 resource stock, 0 offspring, age 0) on the landscape cell of their parent (Figure 11).

Links between parameters

In this study, I set the reproduction cost to the same value as the maintenance cost, assuming that is similarly costly to survive and reproduce for animals. It can also be interpretated as an individual struggling to survive will be less likely to reproduce. Prey *i*'s maintenance cost μ_i is computed such that an animal that has eaten to max consumption at every timesteps between two survival trials would be able to maintain, reproduce and keep stock for the next sequence, following the formula:

$$\mu_i = ceil\ (\frac{\sigma_i * f_{surv}}{3})$$

Predator satiation σ_P is computed such that an animal that has eaten to satiation between two survival trials would be able to maintain, reproduce and keep stock for the next sequence, following the formula:

$$\sigma_P = ceil\ \left(\frac{3 * \mu_P}{f_{surv}}\right)$$

These links are choices of mine for this experiment, they can be set independently otherwise.

3.2.3.3. Parameters table

Table 2. Parameters table. The values noted 'Variable' were modified directly or indirectly during the experiments.

Class	Object	Name	Symbol	Value	Unit
Landscape		Size of the landscape grid	S	25	Cells
		Max resources of type 1	K_1	100	Resource units
		Max resources of type 2	K_2	Variable	Resource units
Animal	Prey 1	initial density	N^{0}_{1}	100	Nb of ind.
		move range		0.1	Fraction of S
		max consumption	σ_1	10	Resource units
		maintenance cost	μ_1	34	Resource units
		reproduction cost	ρ_1	34	Resource units
		fertility	λ_1	1	Nb of ind.
		time of introduction	t_1	0	timesteps
	Prey 2	initial density	N^{0}_{2}	100	Nb of ind.
		move range		0.1	Fraction of S
		max consumption	σ_2	Variable	Resource units
		maintenance cost	μ_1	Variable	Resource units
		reproduction cost	ρ_2	Variable	Resource units
		fertility	λ_2	Variable	Nb of ind.
		time of introduction	t_2	0	timesteps
	Predator	initial density	P^{0}	100	Nb of ind.
		move range		0.1	Fraction of S
		satiation	σ_P	Variable	Resource units
		maintenance cost	μ_p	Variable	Resource units
		reproduction cost	ρ_P	Variable	Resource units
		fertility	λ_p	0.5	Nb of ind.
		time of introduction	t_P	200	timesteps
		catch probability of prey 1	$p^{catch}{}_{1}$	0.1	-
		conversion rate of prey 1	Υ_1	100	Resource units
		catch probability of prey 2	$p^{catch}{}_{2}$	Variable	-
		conversion rate of prey 2	Υ_2	Variable	Resource units
Other		Simulation time	t_{max}	1000	Timesteps
		Frequency of survival trials	f_{surv}	10	Timesteps
		Freq. of reproduction trials	f_{repr}	10	Timesteps
		Frequency of landscape refill	f_{fill}	10	Timesteps

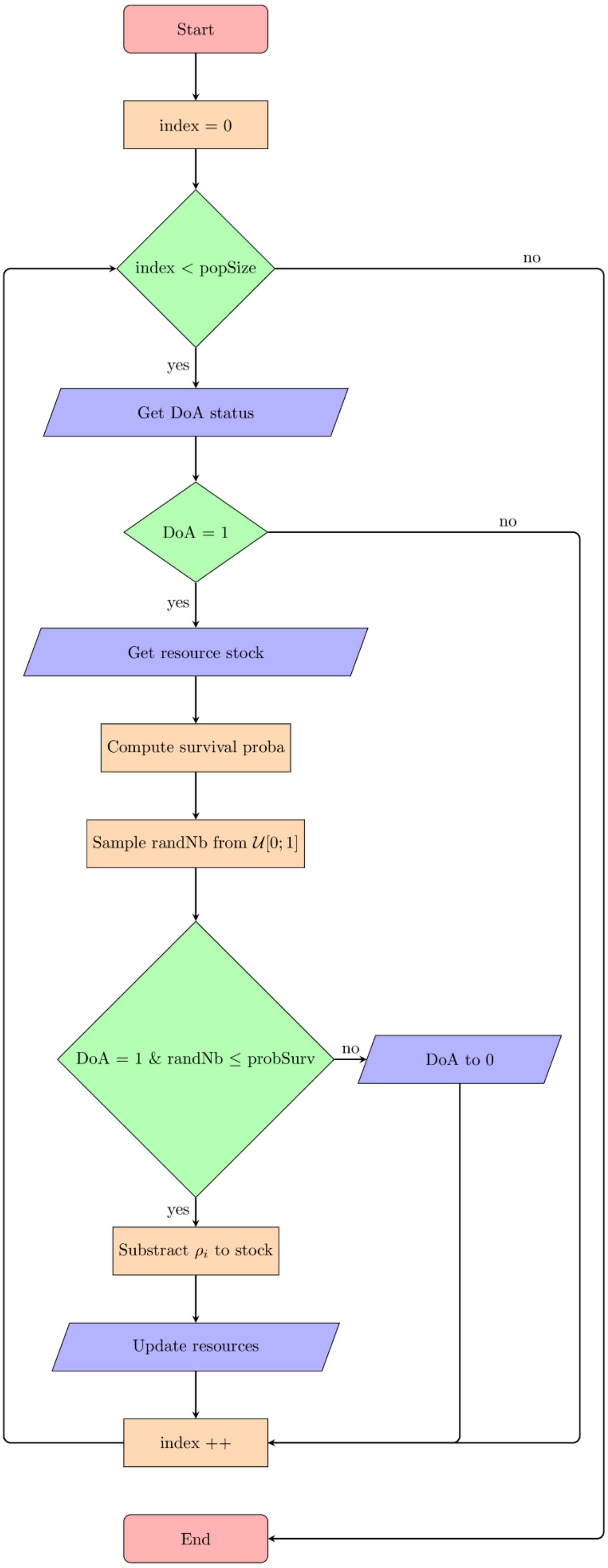

Figure 7. Flowchart of the animal survival trial sub model. Rectangular boxes indicate internal processes. Oblique boxes indicate processes with input or output. Diamond boxes indicate conditional processes. 'DoA' = dead or alive.

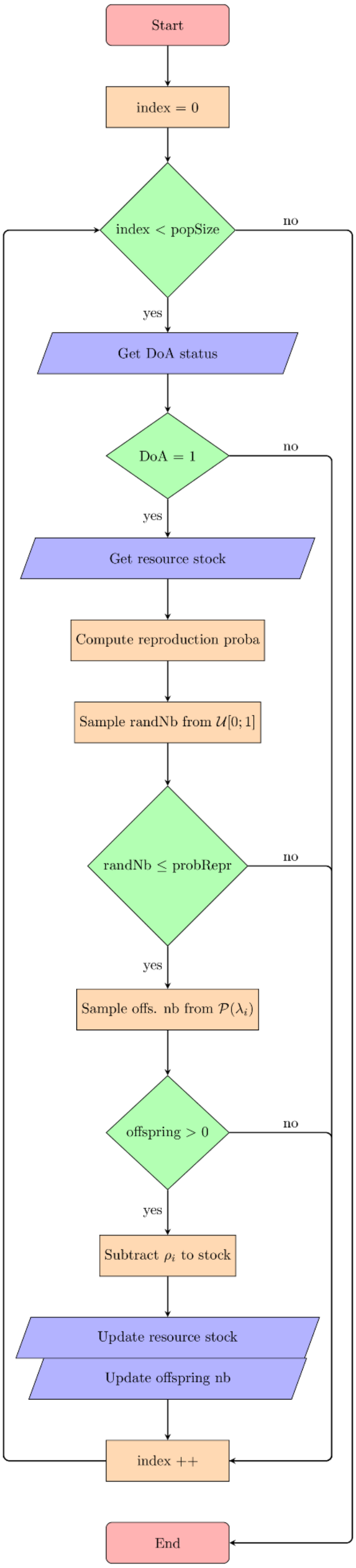

Figure 8. Flowchart of the animal reproduction trial sub model.

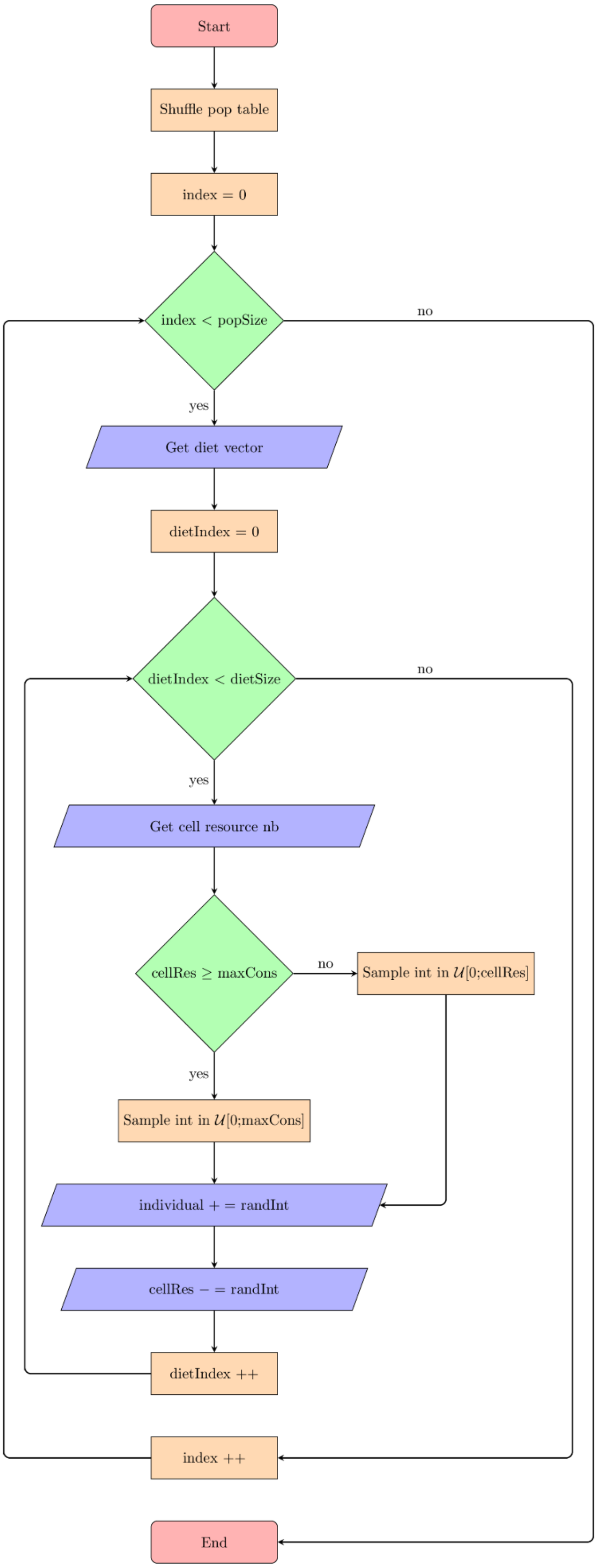

Figure 9. Flowchart of the prey feeding sub model.

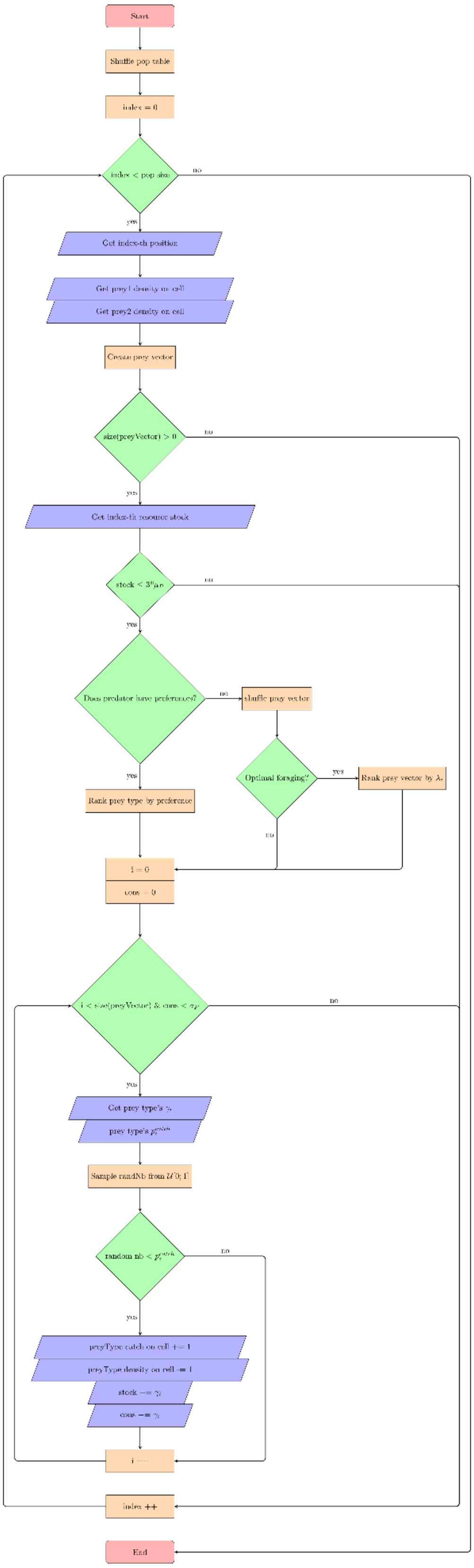

Figure 10. Flowchart of the predator hunting function. Online pdf version here.

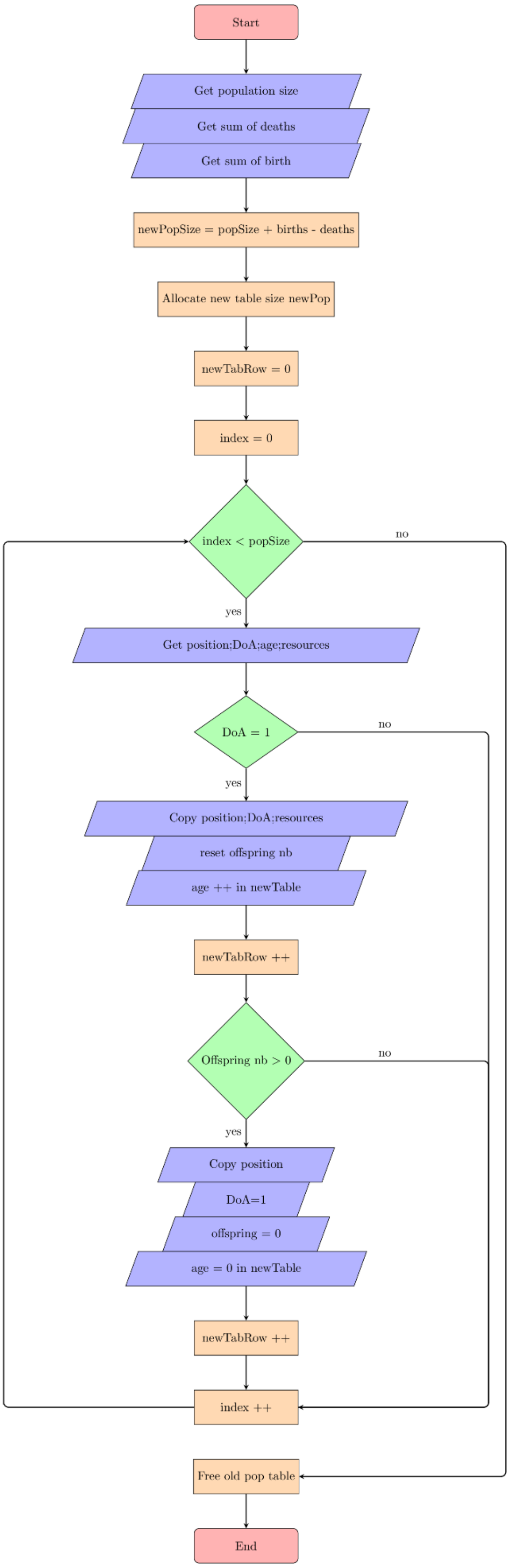

Figure 11. Flowchart of the sub model updating the animal population tables.

3.2.4. Programming/coding

The model was coded in C++. This object-oriented language was well suited to this work, notably thank to classes and derived classes. Each class (landscape and animal population) set common characteristics and functions that are shared with derived classes. Then, it is easier to add a new kind of entity (prey, predator, or another layer of landscape) as a derived class, with the same characteristics as the parent class but with additional characteristics or functions. For example, predator and prey are derived classes of the animal class, their share the basic characteristics and functions of any animal in the model (movement, reproduction, survival, building functions, etc) but differ by their resource absorption functions (feeding for prey and hunting for predator) and some additional characteristics (predator have a number of resources per catch and a catch probability for each prey type). Creating another trophic layer of animals with different feeding behaviour then consisted in adding the functions and characteristics that make it different from prey and predator, as they would inherit all the animal basic functions of the animal class, as well as a new entry in the diet table. Creating objects of each derived class was more straightforward, as they share the same parameters and functions and differ by the parameter values and functions arguments. For example, prey 1 and prey 2 share the exact same parameters and functions but only differ by the parameter values (e.g., prey 1 has a higher fertility than prey 2, prey 2 relationship between resource stock and survival probability is logistic and prey 1 is exponential negative). C++ is also optimised to iterate through loops over different objects of the same class (different populations of prey) to apply the same function(s). For example, make all prey population move iteratively, then feed iteratively, etc…

Using this type of optimised structure, coupled with allocating population tables information to neighbouring locations in the memory, made computation faster. Simulating around 4000 animals interacting on 625 cells during 1000 timesteps (100 generations) took 7 to 12 seconds on average (excluding extinctions) according to population dynamics parameter values on an Intel® Core™ i5-7500 CPU @ 3.40GHz. The parameter that most strongly influenced computing time was the size of the landscape (the value of 25 was a good trade-off between landscape size and computing time) and the frequency of append to the results files.

The model was run from the Linux command line using a bash script that sets the parameter values, compiles, and runs multiple simulations in for loops, setting the seed to a different value at random at each call of the model. A text file is created for each set of simulation replicates to save the parameter values, appending the seed and the simulation time at each call. Re-running a simulation with the same parameter values and the same seed will give the exact same results, which can be handy for problem-solving.

The history of model versions, with the commented code of the model and associated simulation-launching scripts can be found on my GitHub (https://github.com/AdrianBach/abmClean.git).

3.3.Methods

To verify the reliability of the model, I calibrated the model's parameters to find a stable case of trophic interactions between two prey populations with similar characteristics, a predator population, and symmetrical predation to have a baseline level of apparent competition, both prey populations undertaking predation to the same extent. Then I generated asymmetry in predation by varying the characteristics hypothesised to induce apparent competition in prey 2 while keeping these characteristics fixed for prey 1. I measured the changes in prey 1 dynamics to evaluate the relative change in the apparent competition effect. In addition to testing the model against the mathematical theory underpinning apparent competition, it also demonstrates the relative impact of a multitude of parameters on the intensity of apparent competition in my model.

3.3.1. Simulations

All simulations were run over 100 generations (1 generation = f_{surv} = 10 timesteps). Predators were introduced after 20 generations to allow a period of burn-in time for prey to stabilise around pseudo-carrying capacity. 30 replicates were simulated for each parameter set to show the range of the outcomes. Each population's density at each generation was averaged over the replicates and a boot-strapped 95% confidence interval was computed around them. This allowed to plot the evolution of the populations mean density and confidence intervals over generations for each set of replicates. All simulations were run with the model version v0.5.9, available for consultation at this link. The analyses were run on R (v4.2.1; R core team (2022)).

3.3.2. Calibration

Preliminary model exploration revealed that prey characteristics were less critical for affecting stability than the predator ones. I chose a value of 100 for parameters in resource units or number of individuals to be able to easily interpret parameter values as fractions of one another. With the prey 1 parameters in Table 2 applied to both preys, the simulations resulted in a carrying capacity of 1,654 [1,642 ; 1,665] (bootstrapped 95% confidence interval) preys 1 and 1,647 [1,637 ; 1,656] preys 2 in absence of predators. This might be conceptualised, e.g., as two similar populations of herbivores in a protected area. Then I ran a full factorial design (as in Thiele, Kurth and Grimm (2014)) to explore several ranges of values for the predator characteristics while keeping the prey resources per catch Υ_i to 100 units. First, I spanned very large ranges of predator maintenance cost μ_p, prey catch probability p^{catch}_i and predator fertility λ_P to eliminate unlikely scenarios and narrow the ranges. Finally, μ_p varied from 100 (survival and reproduction largely assured by one catch each timestep) to 1,000 (one catch per timestep only guaranties survival) by 100 units increments. p^{catch}_i ranged from 0.1 (relatively difficult for predators to reach satiation) to 0.5 (very easy for predators to reach satiation) by 0.1 increment. Predators' λ_P was fixed to 0.5. With 10 replicates per parameter set, the narrowed calibration experiment was 300 simulations. The most suitable parameter set was chosen by plotting the dynamics of predators and prey and choosing the parameter values that produced the most stable populations with the highest final density of predators. This parameter set was the baseline scenario for the sensitivity analysis.

3.3.3. Sensitivity Analysis

Prey 1 parameters were fixed to the values in Table 2, while prey 2 parameters varied across a range of plausible values following a one-factor-at-a-time approach (as in ten Broeke, van Voorn and Ligtenberg (2016)). I varied population-level parameters that would induce asymmetry in predation and therefore apparent competition, by varying the asymmetry between prey population growth rates, prey population carrying capacities, predator population numerical and functional response according to prey species (Table 3).

3.3.3.1. Fertility

Changing the fertility (λ_i) can be interpreted as introducing a competing prey (prey 2) that reproduces in a larger quantity, or managers helping prey 2 to get more or less offspring, than the focal prey (prey 1). The fertility parameter is expected to impact the competing prey's growth rate. Prey 2 fertility was varied across the values 0.1, 0.5, and from 1 to 10 by increments of 1. A λ_2 of 1 being the same as prey 1; the baseline scenario. A prey 2 with lower fertility than prey 1 ($\lambda_2 < \lambda_1$), is expected to produce fewer offspring, decreasing prey 2 final density, thus sustaining fewer predators, which in turn should alleviate predation on prey 1 and increase its final density. With a $\lambda_2 > \lambda_1$, all the opposite is expected.

3.3.3.2. Maximum consumption

Changes in the maximum consumption value can be interpreted as introducing a prey 2 that exploits its unique non-overlapping resource more or less efficiently than prey 1 population. Prey 2 maximum consumption was varied from 5 to 30 by increments of 5, plus the extreme value of 50, the baseline scenario value being 10 resource units. A prey 2 with $\sigma_2 < \sigma_1$ is expected to have a higher pseudo-carrying-capacity, as more animals can be maintained with the same amount of resources, thus increasing prey 2 final density, thereby sustaining more predators, which in turn should increase predation on prey 1 and decrease its final density. With a $\sigma_2 > \sigma_1$, all the opposite is expected.

3.3.3.3. Resource abundance

Varying this parameter of maximum resource abundance can be interpreted as a loss or gain of resources for prey 2 but not prey 1 due to environmental reasons, or to managers providing supplementary feeding or suppressing part of the food source. Prey 2 maximum consumption was varied from 50 to 200 by increments of 50, plus the extreme values of 300 and 500, the baseline scenario value being 100 resource units. This is another way to influence prey 2's carrying capacity, so we expect the same outcome as the maximum consumption experiment.

3.3.3.4. Catch probability

Varying the catch probability parameter could be interpreted as providing shelter to prey 2 but not prey 1, introducing a prey 2 that is more easily caught by predators than prey 1 (e.g., introduction of a naïve prey or setting traps) or, more generally, introducing a predator with a stronger or weaker functional response for prey 2 than for prey 1. Prey 2 catch probability varied from 0.1 to 0.5 in 0.1 increments, 0.1 being the baseline value. A prey 2 with $p^{catch}_2 > p^{catch}_1$ will be caught more often, making it easier for predators to reach satiation, but at the same time, will be more likely to be depleted by over predation, thereby decreasing the number of available preys. So, if p^{catch}_2 is too high, predator population density and predation pressure on prey 1 would decrease, resulting in an increase in prey 1 final density.

3.3.3.5. Resources per catch

Changes in the resources per catch parameter can be interpreted as introducing a prey 2 that is more or less nourishing to predators than prey 1, or for which the predator needs to spend more or less energy handling than prey 1. It is also equivalent to introducing a predator with a stronger or weaker numerical response for prey 2 than for prey 1. The amount of resource that predator gets from catching a prey 2 varied from 50 to 300 by increments of 50, plus the extreme value of 500, the baseline scenario value being 100 resource units. A $\Upsilon_2 < \Upsilon_1$ will increase the number of catches needed for predator to maintain but since the catch probabilities stay the same, it should reduce the final density of predators and increase both preys' final density.

Table 3. Parameter ranges chosen for the sensitivity analysis.

Parameter	Baseline	Min	Max	Increment	Extreme values
λ_2	1	1	10	1	0.1 ; 0.5
σ_2	10	5	30	5	50
K_2	100	50	300	50	500
p^{catch}_2	0.1	0.1	0.5	0.1	-

ϒ2	100	50	300	50	500

3.3.3.6. Measures

As an overview of the changes in predator and prey population dynamics, I have measured the mean final density of each population N^*_i as the density over the last 25 generations averaged across the replicates. I have also measured the mean amplitude of the oscillations as the difference between the maximum and minimum density over the last 25 generations averaged across the replicates. In presence of oscillations in densities, this approach avoided the artifact of measuring the final density when the last 25 generations do not exactly cover a full multiple of a complete cycle. Indeed, interpreting an average final density as an equilibrium point without considering the shape and size of oscillations can be misleading (Abrams, Holt and Roth, 1998).

To assess the change in apparent competition intensity on populations, I measured the population's mean final density deviation from its value in the baseline scenario (e.g., dN_1^*, in fraction of N^*_1 in the baseline scenario for prey 1) excluding the replicates that resulted in an extinction.

$$\text{e.g.,} \qquad dN_1^* = \frac{N_1^* - N_{1,baseline}^*}{N_{1,baseline}^*}$$

I also measured the change in the amplitude of density oscillations in each case as the deviation from the amplitude of oscillations in the baseline scenario (dA_1^*, in fraction of A^*_1 in the baseline scenario), excluding the replicates that resulted in an extinction.

$$\text{e.g.,} \qquad A_1^* = \max(N_1^*) - \min(N_1^*)$$

$$\text{e.g.,} \qquad dA_1^* = \frac{A_1^* - A_{1,baseline}^*}{A_{1,baseline}^*}$$

The extinction frequency was also computed, as the number of extinction events over the replicates. To link the apparent competition effect to predation, I have estimated the mean catch rate CR_i of each prey population i as the number of catches during the timestep of the survival and reproduction trials over the density after survival and reproduction trials, averaged over the replicates.

$$CR_i(t_{surv}) = \langle \frac{catches_i(t_{surv})}{N_i(t_{surv})} \rangle$$

The growth rate of each population was estimated as the difference between the density after trials and the density after the previous trials over the density after the previous trials.

$$\text{e.g.,} \qquad r_1(t_{surv}) = \frac{N_1(t_{surv}) - N_1(t_{surv} - f_{surv})}{N_1(t_{surv} - f_{surv})}$$

3.3.4. Predator functional and numerical responses

To follow the shape of the predator functional and numerical responses, I plotted the predator realised growth rate and the prey populations catch rate against the prey populations realised growth rate in relevant cases.

3.4. Results

3.4.1. Calibration

3.4.1.1. Large exploration

Regardless of predator maintenance cost μ_P and catch probability p^{catch}, increasing predator's average number of offspring (fertility) λ_P slightly increased the predators' final density P^* but also generated oscillations in predator population dynamics, which caused predators extinctions in some cases. Oscillations happened because, as predators produced more offspring, predation pressure increased and drove the prey populations to too low of a density to maintain the predator population. Predator population density declined through starvation because preys were too scarce. Because of the low number of predators, prey population densities increased again, which allowed more predators to catch enough prey to reproduce. Predator population increased, and the cycle repeated itself. A fertility value of $\lambda_P = 0.5$ resulted in the most stable predator-prey population dynamics (predators produce half as many offspring as preys). This is consistent with ecological theory, which predicts that dynamics are more stable when preys reproduce faster than the predators (Barraquand *et al.*, 2015; Serrouya *et al.*, 2015).

A $p^{catch} \geq 0.5$ caused too fast of a prey population decline and systematically drove predator and prey populations to extinction. I narrowed the p^{catch} range to [0.1 ; 0.5]. A predator's maintenance cost $\mu_P \leq 100$ resource units made it too easy for predators to survive and reproduce, consequently increasing their population too rapidly for preys to sustain. The increased predation pressure systematically caused prey populations decline and drove the predator population to extinction. A μ_P up to 1,000 units produced stable cases when the catch probability was high enough to compensate for the difficulty to survive and reproduce for predator. Nevertheless, P^* was low for high μ_P, the predator population was hardly maintaining itself at the density at introduction. The $\mu_P = 300$ units were the most promising results, I narrowed the μ_P range to [200 ; 700] units.

3.4.1.2. Narrow exploration

Like the previous section, a $p^{catch}_i > 0.2$ drastically increased the frequency of extinctions. For low μ_P values, for which survival and reproduction trials were easier to pass, predators depleted the prey to extinction before going extinct themselves. For higher μ_P values (challenging survival and reproduction), the predator would drive the prey populations to very low values unable to sustain predators and went extinct. After that, the remaining prey populations settled back to carrying capacity due to the absence of predation. In some cases (e.g., μ_P = 200 / p^{catch} = {0.2 ; 0.3} or μ_P = 300 / p^{catch} = {0.3 ; 0.4}), the two prey populations end up at a different final densities N^*_i while they were expected to endure predation to the same extent. This happened when prey populations were depleted to very low numbers and, by chance, either one of the preys was driven extinct while the other persisted and grew back to carrying capacity. The prey that persisted by chance hence had a higher mean N^*_i over the replicates. Likewise, as μ_P value increased, it was more difficult for predators to survive and reproduce. When the $p^{catch}{}_i$ value was high enough to compensate for a high μ_P by making easier to catch prey and low enough not to deplete them, increasing μ_P decreased P^*, otherwise predator population went extinct. The μ_P = 300 and p^{catch} = 0.1 parameter set was the most stable for the highest P^*. I chose it as the baseline parameter set for the next experiment (Figure 12).

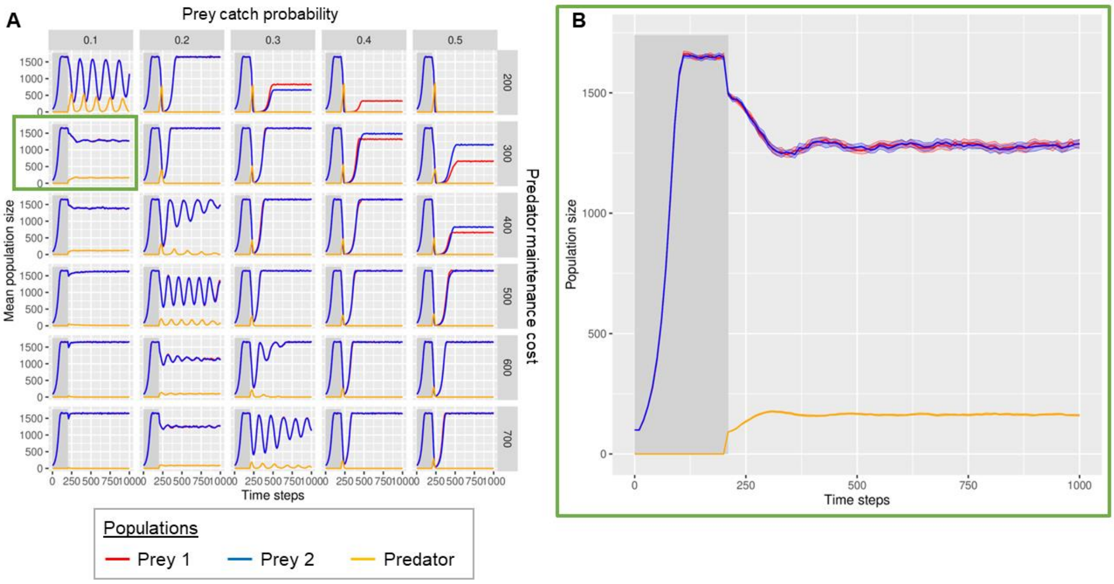

Figure 12. Results of the narrowed parameter exploration. (A) evolution of the prey 1, prey 2 and predator population mean densities along timesteps according to the prey catch probability in x and maintenance cost in y. (B) Detail of the chosen parameter set for the baseline scenario. The coloured ribbons are the bootstrapped 95% confidence intervals. The grey shaded areas cover the time preceding predator introduction.

3.4.2. Sensitivity analysis

3.4.2.1. Fertility λ_2

As expected, increased asymmetry in the preys' fertility resulted in an asymmetry in the preys' growth rate when densities increased from rare, or intrinsic growth rate. For example, when prey 1 intrinsic growth rate at generation 3 was 0.42 with a [0.39 ; 0.44] bootstrapped 95% confidence interval, prey 2's was 0.69 [0.65 ; 0.72] for λ_2=3 and 0.26 [0.26 ; 0.29] for λ_2=0.5. It also generated a slight asymmetry in prey's carrying capacities when prey 2 was more fertile than prey 1 ($\lambda_2 > \lambda_1$); prey 1 density had stabilised to 1,644.87 [1,634 ; 1,654.97] before predator introduction while prey 2's had stabilized at 1,739.5 [1,723.97 ; 1,754.53] for λ_2=3.

The only extinctions observed were in the predator population, and these happened for a prey 2 with a very low fertility λ_2=0.1 with a frequency of 0.07 (i.e., 2 predator population extinction events out of 30 replicates). These extinctions were caused by the decline in the prey 2 population density (down to -39.23% [-40.53 ; -37.92]) that could not produce enough offspring to compensate for predation. As the prey 2 population declined, the predators were short on prey for consumption and started also declining until eventual extinction.

When $\lambda_2 < \lambda_1$, the prey 2 population endured the same predation pressure as prey 1 (Figure 13 panel B) but recovered more slowly as it produced fewer offspring. The decline of prey 2 caused prey scarcity for predators, and predator population size consequently decreased, alleviating predation pressure on prey 1, the density of which thus increased (Figure 13 panel A). Moreover, the increase in prey 1 density due to predation relief was lower than the decline in prey 2. For example, in λ_2 = 0.1, the density deviation from baseline scenario was +21.21% [20.89 ; 21.54] for prey 1 and -39.23% [-40.53 ; -37.92] for prey 2, and +4.74% [4.34 ; 5.11] for prey 1 and -14.19% [-14.61 ; -13.77] for prey 2 in λ_2 = 0.5. Thus, the overall number of prey available was lower than the baseline scenario, hence a lower predator final density. There was no notable change in the amplitude of oscillations compared to the baseline scenario.

When $\lambda_2 > \lambda_1$, prey 2 population recovered more efficiently from predation than prey 1 as it produced more offspring. Indeed, prey 2 stabilised at a higher density than prey 1. This higher density sustained more predators, which in turn decreased the prey 1 population final density due to a higher predation pressure than baseline scenario (Figure 13). The total amount of available prey for the predator was slightly superior than baseline scenario at every increase of λ_2 (the highest gap being with the extreme value of λ_2=10 and was -29.86% [-30.81 ; -28.97] for prey 1 and +36.18% [35.7 ; 36.7] for prey 2, which is much closer than for the $\lambda_2 < \lambda_1$ case). Combined to the higher fertility of prey 2, this positive gap resulted in the predator density to plateau at a higher P^* (from 164 [161 ; 168] animals on average in baseline scenario to 231 [219 ; 241] with the extreme value of λ_2=10, or an increase of 41.23% [39.84 ; 42.7]). This increase resulted in a significant drop in prey 1 population final density; from -11.4% [-11.83 ; -10.99] for $\lambda_2 = 2$ to -30.53% [-31.25 ; -29.86] for $\lambda_2 = 9$. The oscillation amplitude in prey 1 density increased but population density stayed very low: between 860 and 914 animals on average at maximum (λ_2=9).

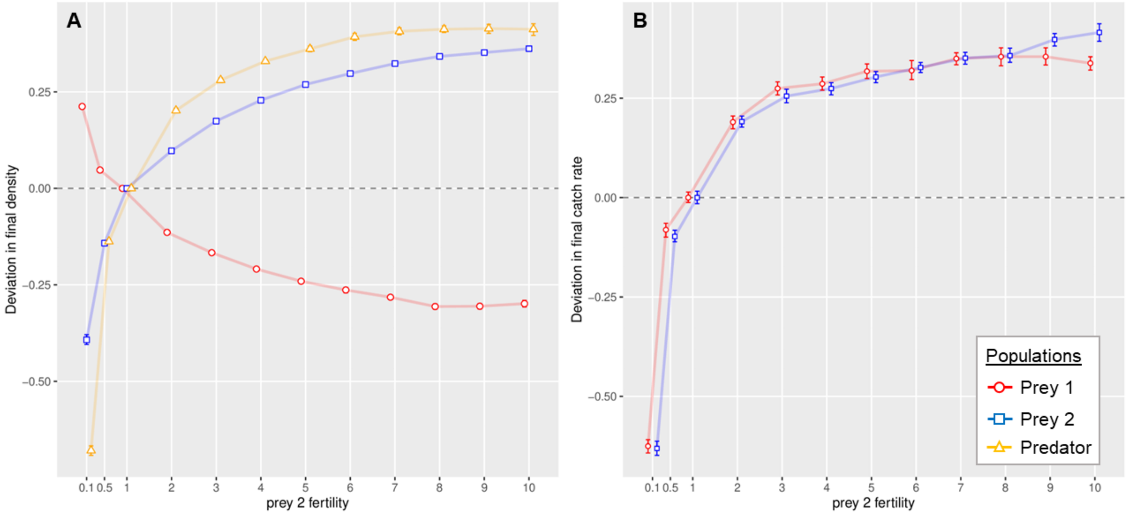

Figure 13. Model sensitivity to asymmetry in prey populations fertility (average number of offspring produced) excluding the replicates that ended in extinction. A prey 2 fertility of 1 is the baseline scenario, symmetrical apparent competition is shown by the grey dotted line. Asymmetry increases as prey 2 fertility differs from the baseline scenario value. (A) Change in population mean densities at the end of the simulation time compared to the baseline scenario (in fraction). (B) Change in the population mean catch rates at the end of the simulation time compared to the baseline scenario (in fraction). The error bars are the bootstrapped 95% confidence interval.

3.4.2.2. Maximum consumption σ_2

Predator population extinctions were increasingly frequent given a prey 2 with a high consumption rate ($\sigma_2 \geq 25$ resource units); from 20% of the replicates with $\sigma_2 = 25$ units, to 100% with the extreme value of $\sigma_2 = 50$ units. Indeed, as σ_2 increased, the landscape resource pool for prey 2 could maintain fewer of its members, causing their carrying capacity to be at a lower density. Their scarcity made fewer available prey for predators, meaning that predator density subsequently decreased, eventually to extinction. Even if the predation relief on the prey 1 population increased their final density N^*_1 (up to +27.81% [27.53 ; 28.08] for $\sigma_2 = 50$), they could not compensate for the lower N^*_2 (down to -61.04% [-60.8 ; -64.43] for $\sigma_2 = 50$). It is most likely because the increase in prey 1 population density was capped by the landscape carrying capacity. This made the overall number of available preys lower as σ_2 value increased, because the drop in prey 2 final density was superior to the increase of prey 1's in absolute values (Figure 14). The impact on the amplitude of the oscillations in density was very weak.

Given a prey 2 consuming less of its resource per timestep than prey 1 ($\sigma_2 < \sigma_1$), prey 2 carrying capacity (3,376 [3,365 ; 3,388] animals on average) was much higher than prey 1's (1,636 [1,626 ; 1,646] animals on average), making the overall number of prey available much higher than the baseline scenario. This generated strong oscillations (6.96 [6.87 ; 7.04] times larger than baseline for prey 1 and 14.61 [14.49 ; 14.74] times larger for prey 2]). The large number of available preys sustained a high density of predators, which subsequently resulted in over predation, decreasing the densities of both prey populations. Predator numbers subsequently followed, and the low σ_2 allowed prey 2 population to recover faster and the cycle started again (Figure 14). Note that, while the average final predator density P* was overlapping with that of the baseline scenario, the predator population oscillated strongly and very close to extinction here (Figure 15). For prey 1, apparent competition with prey 2 drove N^*_1 down by -26.72% [-28.28 ; -25.12].

Something that might be misleading here is that, for σ_2 = 5 units, P* and the final catch rate of the preys overlapped with those of the baseline scenario but prey population average final density still dropped by -26.72% [-28.28 ; -25.12]. The important change at this σ_2 value was the amplitude of the oscillations in densities (Figure 14 and Figure 15). Cycling between 491.37 and 1,474.36 members of prey population 1 on average caused the final N^*_1 to be lower than the baseline scenario.

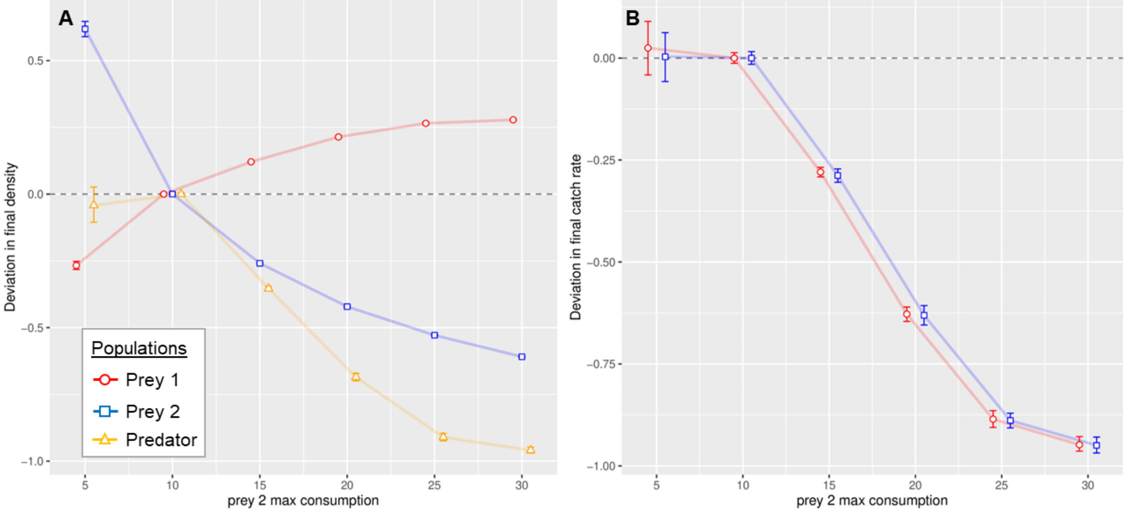

Figure 14. Model sensitivity to asymmetry in prey populations maximum consumption parameter, excluding the replicates that ended in extinction. The value of 10 resource units is the baseline scenario, which result is shown by the grey dotted line. Asymmetry in maximum consumption increases as prey 2 maximum consumption differs from the baseline scenario value. (A) Change in population mean densities at the end of the simulation time compared to the baseline scenario (in fraction). (B) Change in the population mean catch

rates at the end of the simulation time compared to the baseline scenario (in fraction). The error bars are the bootstrapped 95% confidence interval.

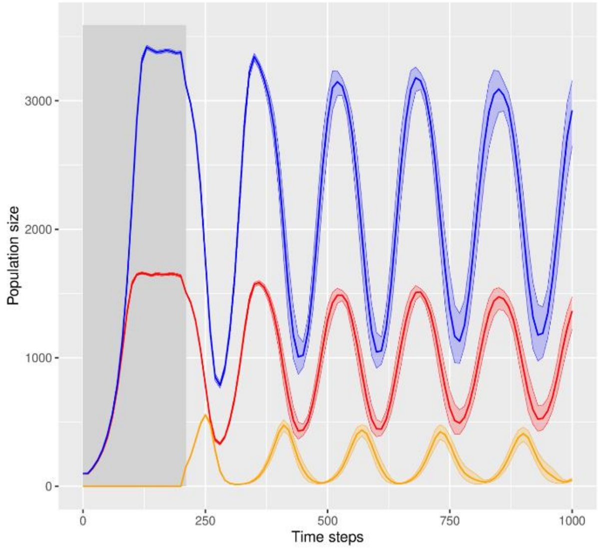

Figure 15. Evolution of the populations mean density along simulation timesteps for a prey 2 max consumption of 5 resource units (higher carrying capacity for prey 2 than prey 1). The colour shaded areas are the bootstrapped 95% confidence intervals around the means. The grey shaded area covers the timesteps preceding predator introduction.

3.4.2.3. Resource abundance K_2

Predator population extinction was consistent for the two extreme values of K_2 = {300 ; 500}, for which prey 2's carrying capacity was very high (around 5,000 and over 8,000 animals for K_2 = 300 and K_2 = 500, respectively). High prey 2 carrying capacity provided too many preys for predators to consume, which depleted the prey immediately after their introduction (even to extinction for prey 1 population in one third of the replicates with K_2 = 500), leading to a rapid crash of the predator population.

When prey 2 had less abundant resources than prey 1 ($K_2 < K_1$), the final population density of both prey populations quickly plateaued at their respective pseudo-carrying capacities (N^*_2 = 727 [721 ; 734] animals, N^*_1 = 1,562 [1,549 ; 1,576] animals), which adds up to less than the baseline scenario's overall number of available preys. Predator density thus stabilised at a lower P* than their density at introduction (47 [43 ; 50] animals). This very stable situation might be due to prey populations being very close to carrying capacity and undertaking a very low and constant predation pressure. Apparent competition thus increased N^*_1 by 21.95% [21.53 ; 22.4] (Figure 16).

When prey 2 had more resources available than prey 1 ($K_2 > K_1$), a higher prey 2 pseudo-carrying capacity allowed a higher density of prey 2, which therefore sustained a higher number of predators, intensifying predation on prey 1 and decreasing N^*_1 by up to -29.74%

[-31.29 ; -28.14] for K_2 = 200. Higher prey 2 carrying capacities also generated stronger oscillations (up to 6.94 [6.83 ; 7.05] times larger for prey 1 in K_2 = 200) for the same reasons as the case of σ_2 = 5 units in the previous results section. Similarly, the strong increase in the density oscillations amplitude at K_2 = 200 resource units, made predator population cycle very close to extinction, thereby decreasing P* (Figure 16).

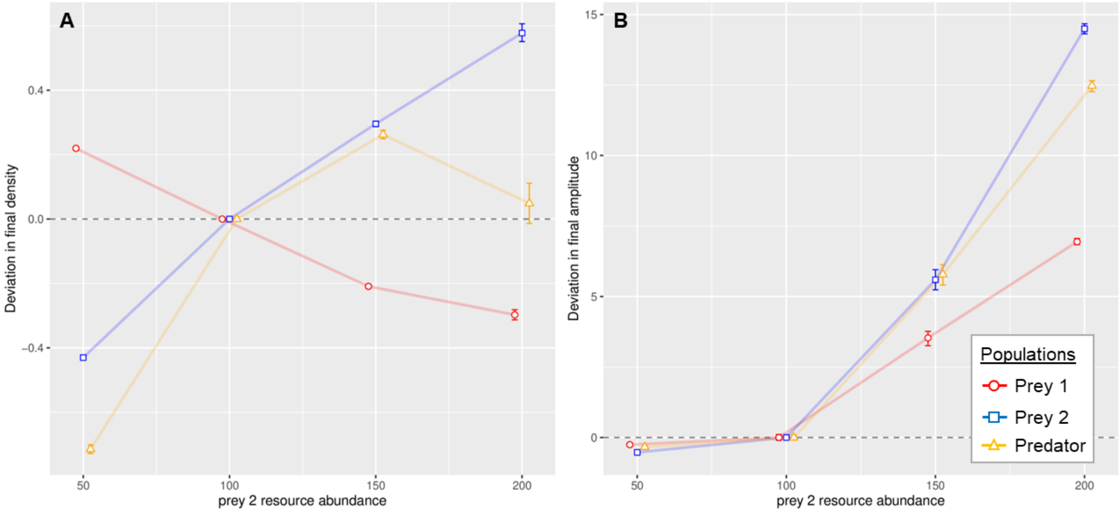

Figure 16. Model sensitivity to asymmetry in prey populations resource abundance, excluding the replicates that ended in extinction. The value of 100 resource units is the baseline scenario, which result is shown by the grey dotted line. Asymmetry in resource abundance increases as prey 2 resource abundance differs from the baseline scenario value. (A) Change in population mean densities at the end of the simulation time compared to the baseline scenario (in fraction). (B) Change in the amplitude of density oscillations at the end of the simulation time compared to the baseline scenario (in fraction). The error bars are the bootstrapped 95% confidence interval.

3.4.2.4. Catch probability p^{catch}_2

Predator population extinctions were increasingly frequent when $p^{catch}_2 \geq 0.3$; from 43% of the replicates with p^{catch}_2 = 0.3 to 100% with p^{catch}_2 = 0.5. In these cases, the predators depleted prey 2 population very quickly (even to extinction of prey 2 in 23% of the replicates for p^{catch}_2 = 0.5) and then could not sustain on prey 1 only.

Increasing p^{catch}_2 increased the catch rate on prey 2, which led to N^*_2 decreasing by up to -53.89% [-57.71 ; -50.53], thus sustaining fewer predators and resulted in an increase of up to +11.71% [10.84 ; 12.61] in N^*_1 for p^{catch}_2 = 0.3. Additionally, the increased catch rate on prey 2 greatly reduced the catch rate on prey 1. For example, with p^{catch}_2 = 0.2, the 10.91% [5.97 ; 15.51] increase in prey 2 catch rate, resulted in an drop of -38.46% [-41.08 ; -35.81] in prey 1 catch rate compared to the baseline scenario (Figure 17).

Increasing p^{catch}_2 also increased the amplitude of oscillations (by up to 3.23 [3.07 ; 3.38] times in N^*_1 for $p^{catch}_2 = 0.3$). For the values that did not end up in extinction, the rapid depletion of prey 2 population abated before the extinction of either the predator or prey 2, allowing the prey populations to recover and rise the predator number again, generating cycles.

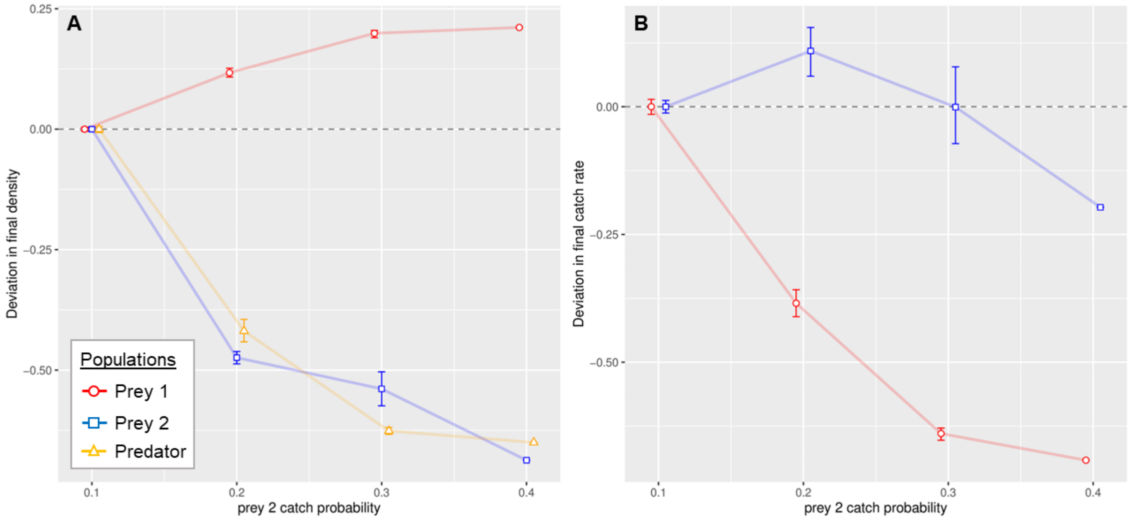

Figure 17. Model sensitivity to asymmetry in prey populations catch probability, excluding the replicates that ended in extinction. The value of 0.1 is the baseline scenario, which result is shown by the grey dotted line. (A) Change in population mean densities at the end of the simulation time compared to the baseline scenario (in fraction). (B) Change in the population mean catch rates at the end of the simulation time compared to the baseline scenario (in fraction). The error bars are the bootstrapped 95% confidence interval.

3.4.2.5. Resources per catch Υ_2

Predator population extinctions were increasingly frequent given a prey 2 highly resourceful as a catch ($\Upsilon_2 \geq 250$ resource units); from 40% of the replicates with $\Upsilon_2 = 250$ units, to 100% with the extreme values of $\Upsilon_2 = \{300; 500\}$ units. In these cases, prey 2 sustained too large of a predation population by facilitating their survival and reproduction, which caused depletion of both prey populations until predators' extinction.

For a prey 2 less resourceful for predator than prey 1 ($\Upsilon_2 < \Upsilon_1$), prey 2 sustained a lower density of predators for the same number of catches, so predator population decreased, alleviating predation on both preys, which increased N^*_1 by 16.55% [16.2 ; 16.92] and N^*_2 by 18.65% [18.31 ; 19] compared to the baseline scenario (Figure 18).

For a prey 2 more resourceful for predator than prey 1 ($\Upsilon_2 > \Upsilon_1$) and Υ_2 up to 200 resources per catch, prey 2 sustained a higher number of predators for the same number of catches. The predation pressure increased on both preys, which decreased N^*_1 by 29.62% [-31.13 ;

-28.15] and N*₂ by 29.47% [-30.59 ; -28.37] for Υ_2 = 200. The oscillation amplitude also increased by up to 6.91 [6.83 ; 7] times for prey 1 and 6.81 [6.7 ; 6.91] times for prey 2 with Υ_2 = 200. When prey 2 population depletion drove predator population down slowly enough to have predation alleviation with no risk of extinction for the predator, both prey populations had time to recover before predation pressure increased again, which generated cycles (Figure 18). In this experiment, increasing Υ_2 makes predators' survival and reproduction easier for the same amount of prey 2 catches, so both prey populations endured the increased predation pressure the same way (Figure 19). Except at Υ_2 = 150 units, where the catch rate for prey 1 is higher than prey 2's with non-overlapping intervals. This is most likely an artifact of averaging over cycles, as Figure 19 shows that the catch rate of both prey populations oscillated in similar ranges at this value for Υ_2.

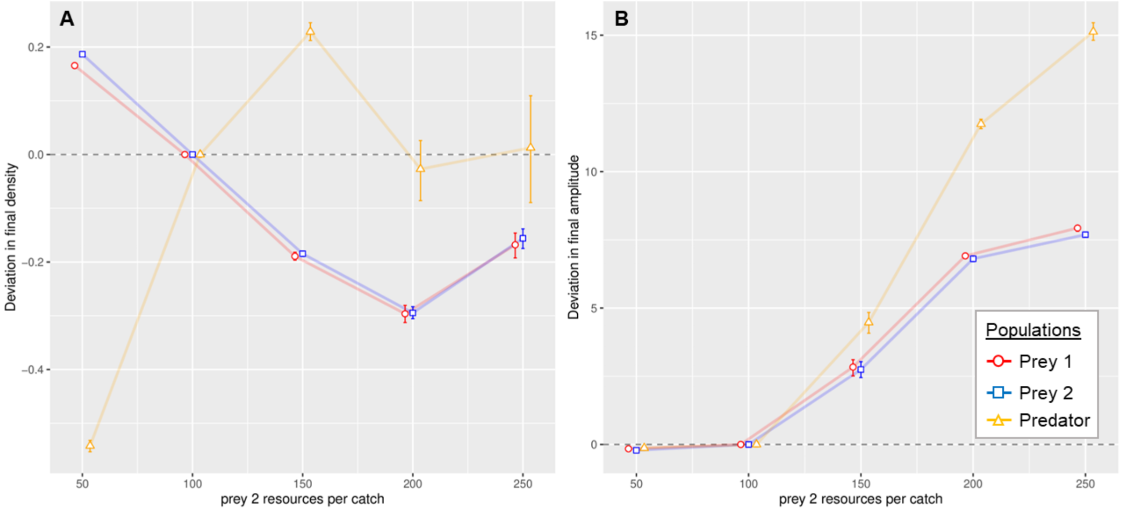

Figure 18. Model sensitivity to asymmetry in prey populations resources per catch, excluding the replicates that ended in extinction. The value of 100 is the baseline scenario, which result is shown by the grey dotted line. (A) Change in population mean densities at the end of the simulation time compared to the baseline scenario (in fraction). (B) Change in the amplitude of density oscillations at the end of the simulation time compared to the baseline scenario (in fraction). The error bars are the bootstrapped 95% confidence interval.

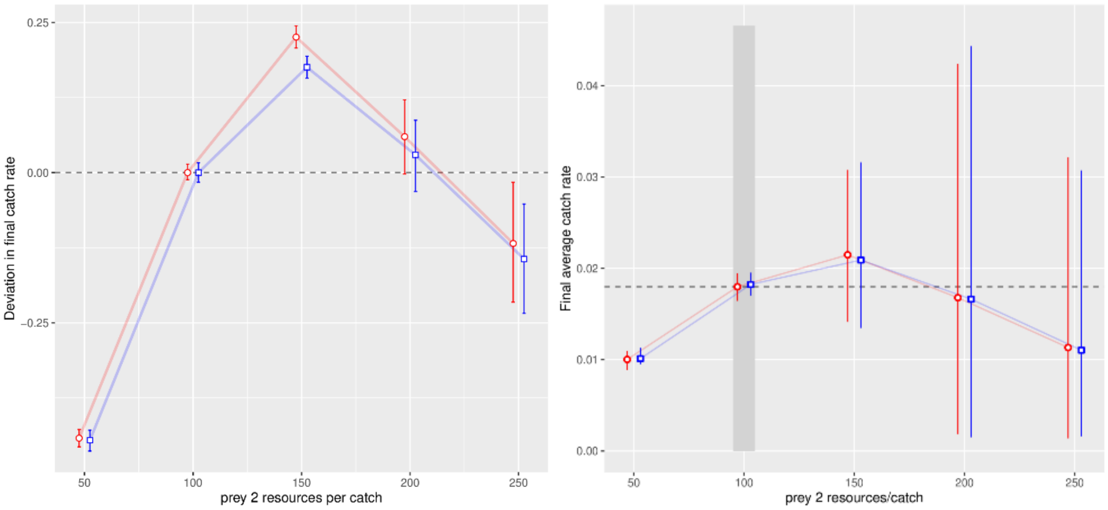

Figure 19. Model sensitivity to asymmetry in prey populations resources per catch, excluding the replicates that ended in extinction. The value of 100 is the baseline scenario, the absence of asymmetry is shown by the grey dotted line. Change in the population mean catch rates at the end of the simulation time compared to the baseline scenario (in fraction). The error bars are the bootstrapped 95% confidence interval. The bars are the amplitude of oscillations, showing the minimum and maximum values reach over the interval in which the final density was computed.

3.4.2.6. Sensitivity

In this section, I compare the intensity of variation in prey 1's extinction frequency, final density, and amplitude of density fluctuations for the same input parameter change (doubling or halving), to determine which input parameter was the focal prey population most sensitive to.

3.4.2.6.1. Effect on prey 1 extinction frequency

Overall, there were very few events of prey 1 population extinction through apparent competition with prey 2 population in the sensitivity analysis experiment (only in 33% of the replicates with the extreme value of K_2=500 resource units). Even if the population was driven to very low densities in some extreme cases, the simulations more frequently end up in predators' extinction first and prey population densities would recover. Hence, in the general case chosen here prey 1 extinction probability frequency to the input parameters variation was low.

3.4.2.6.2. Effect on prey 1 final density

Excluding the parameter value combinations that resulted in an extinction, the fastest and strongest negative effect of asymmetrical apparent competition on prey 1 was the asymmetry between prey populations' maximal resource consumption σ_2. Given a prey 2 consuming its resources twice as slower as prey 1; changing σ_2 from 10 to 5 resource units resulted in a -26.72% [-28.28 ; -25.12] drop in N^*_1 (Figure 14). The resource abundance K_2 followed, which, when prey 2 had twice as many resources at disposal as prey 1 (from 100 to 200 resource units) resulted in a -29.74% [-31.29 ; -28.14] drop in N^*_1 (Figure 16). Then came the resource per catch, a prey 2 twice as much resourceful to predator than prey 1 (Υ_2 from 100 to 200) had a strong negative effect through symmetrical apparent competition, with a -29.62% [-31.13 ; -28.15] drop in N^*_1 (Figure 1618). The slowest and lowest negative effect of asymmetrical apparent competition was when doubling the prey 2 fertility λ_2 from 1 to 2 with a -11.4% [-11.83 ; -10.99] drop in N^*_1 (Figure 1313).

The fastest and strongest positive effect of asymmetrical apparent competition was when prey 2 resource were twice as less abundant as prey 1 (K_2 from 100 to 50 resource units) with a 21.94% [21.53 ; 22.4] increase in N^*_1 (Figure 18). Again, the slowest and lowest positive effect of asymmetrical apparent competition was when prey 2 was twice as less fertile (λ_2 from 1 to 0.5), which resulted in a +4.74% [4.35 ; 5.12] increase in N^*_1 (Figure 13).

The parameters directly influencing the difference between prey 2 and prey 1 carrying capacities appeared to have the strongest impact on apparent competition intensity on prey 1, while the parameter influencing the difference between the preys' growth rate appeared to have the weakest impact on apparent competition. This is most likely because prey fertility's impact on the overall number of available preys was rather weak (e.g., for $\lambda_2 = 3*\lambda_1$, prey 2 carrying capacity was 1,738.91 [1,731.97; 1,746.03] animals and prey 1's was 1,650.82 [1,641.27 ; 1,660.67]), while σ_2 and K_2 impacted it more directly and more strongly. The difference between preys' resources per catch had the strongest symmetrical apparent competition effect by increased predation pressure on both preys without affecting their pseudo-carrying capacities. The impact of the difference in preys' catch probabilities on N^*_1 was significant but less important.

3.4.2.6.3. Effect on oscillations

The difference between the preys fertility had a very low impact on the amplitude of prey 1 density oscillations (0.74 [0.54 ; 0.93] times larger at maximum for $\lambda_2 = 10$ offspring on average). The strongest and fastest impact on oscillations amplitude were again the difference in resources per catches Υ_2, doubling from 100 to 200 units made the amplitude of prey 1 oscillations 6.91 [6.83 ; 7] times larger (Figure 18). Then, a prey 2 consuming twice as less resources as prey 1 (σ_2 from 100 to 50 units) made the oscillations in prey 1 density 6.96 [6.87 ; 7.04] times larger, and a prey 2 with twice as abundant resources than prey 1

(K_2 from 100 to 200 units) made the amplitude of prey 1 oscillations 6.94 [6.83 ; 7.05] times larger. The impact of catch probability on the amplitude of oscillations was less important.

3.4.2.6.4. Shape of relationship between output deviation and input parameter change

When the changes in the parameter values induced an increase in N^*_i compared to the baseline, it was limited by carrying capacity and plateaued, which can explain the nonlinear relationship. As in the experiment with catch probability where N^*_1 plateaus to carrying capacity, or in the fertility experiment where N^*_2 does the same. For parameters influencing prey 2 carrying capacity directly, there was a break between when prey 2 parameter values were under or over prey 1's values, showing what might be tipping points. Prey resources per catch effect on N^*_1 looks quite linear until the value for which predator extinctions started happening.

Table 4. Summary of the sensitivity analysis.

	dev. in N^*_1		Shape of relationship	dev. in amplitude		Shape of relationship
Parameter	min	max		min	max	
λ_2	0.212	-0.298	nonlinear	-0.052	0.74	linear?
σ_2	-0.267	0.278	nonlinear	6.963	-0.382	tipping point
K_2	0.219	-0.297	nonlinear?	-0.254	6.941	tipping point
p^{catch}_2	0	0.211	tipping point	0	3.327	nonlinear
Υ_2	0.165	-0.167	tipping point	-0.157	7.93	nonlinear

3.4.3. Shape of the predator's numerical and functional responses

The examination of the predator's functional and numerical responses shape revealed interesting properties in the model. When plotting the predator growth rate and the preys catch rates as a function of prey densities in the parameter sets that did not exhibit oscillations, the relationship seemed linear, although the densities in stable dynamics varied across a very short spectrum. However, when the system exhibited cycles, the shape of the relationship differed between when prey densities are decreasing (seemingly linear) and when they are increasing (seemingly logarithmical) (Figure 20).

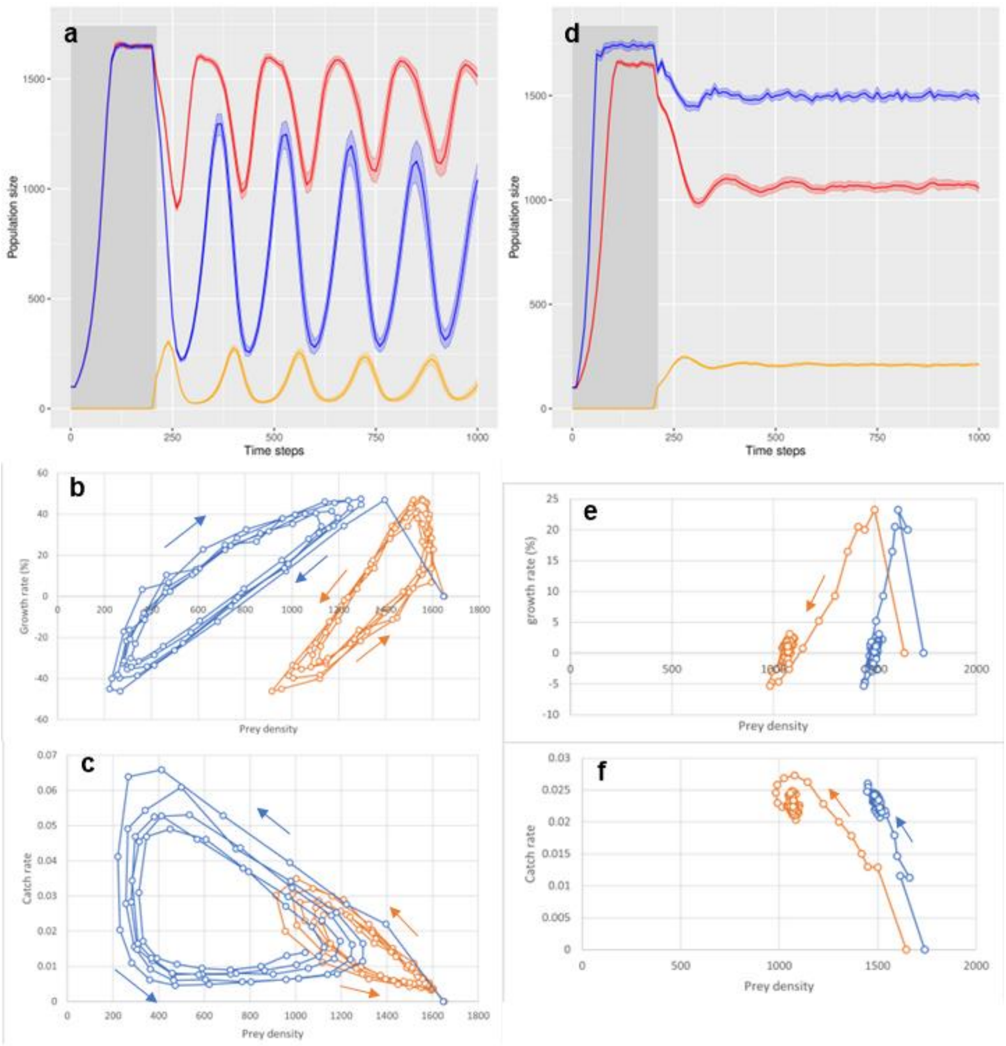

Figure 20. Predator numerical and functional responses in 2 cases of asymmetrical apparent competition. (a) Evolution of the populations mean density along simulation timesteps for a prey 2 catch probability of 0.2 ($p^{catch}_1 = 0.1$) and the associated numerical (b) and functional (c) responses. (d) Evolution of the populations mean density along simulation timesteps for a prey 2 fertility of 0.3 ($\lambda_1 = 1$) and the associated numerical (b) and functional (c) responses. The coloured arrows indicate the direction of variation of the population densities. The colour shaded areas are the bootstrapped 95% confidence intervals around the means. The grey shaded areas cover the timesteps preceding predator introduction.

3.5.Discussion

I introduced an agent-based model (ABM) to simulate the emergence of apparent competition in a trophic system on a spatially explicit landscape lattice. The model was tested in its most fundamental version – with two self-limited prey populations that do not compete for resources but share a predator – against apparent competition (AC) theory. To do so, the parameters influencing asymmetry in predation were varied independently and the resulting change in apparent competition intensity was measured, thereby realising a sensitivity analysis.

3.5.1. Conditions for the emergence of apparent competition

Was sharing a predator sufficient to demonstrate apparent competition in an agent-based model? To test for this, I needed to show that a prey species final density was higher in the presence of just a predator than it was in the presence on both the predator and another prey (Bonsall and Hassell, 1997; Abrams, Holt and Roth, 1998). A challenge was that I could not find a suitable parameter set allowing for a stable system (i.e., no extinction and no large oscillations in densities) in both the absence and presence of a competitor prey species. A predator parameter set that was suitable for predator-prey dynamics in the absence of another prey competitor quickly resulted in extinction when the prey competitor was introduced. Conversely, a predator parameter set that was suitable in a system with both the focal and competitor prey species quickly resulted in the extinction of the predator population when the other prey species was removed, due to a lower total prey density. This situation also happen in real world cases, such as in Roemer, Donlan and Courchamp (2002) which showed that an introduced eagle population could not have sustained only on the local prey species (fox and skunk) in absence of an abundant, predation-resistant, introduced prey species (feral pigs). Yet, in the only parameter set I could find in which all species persisted in both experiments during the calibration simulations ($\mu_P = 200$ resource units, $p^{catch}_i = 0.1$, $\lambda_P = 1$), the focal prey (prey 1 in the experiments) final density was indeed lower in presence than in absence of the other prey (even with identical parameters; around 1400 animals on average when alone with the predator versus around 1000 animals on average with the emergence of large oscillations in presence of the other population), leaning towards symmetrical apparent competition. The simulations in Abrams, Holt and Roth (1998) also exhibited stronger oscillations in the focal prey density when in presence of another, similar competing prey, with a negative effect on the focal prey final density. But finding a suitable parameter set for both experiments was not presented as a challenge in their mathematical, deterministic model. Nevertheless, these results suggest that sharing a predator could be a necessary and sufficient condition for preys to exhibit, at least, symmetrical apparent competition. Also, the agent-based approach to modelling AC revealed that parameterising stable systems is more challenging when increasing realism in the form of mechanistic interactions between discrete agents. Could it suggest that systems of AC between prey species can be more prone to extinction than mathematical models alone would predict?

3.5.2. Sensitivity to asymmetry-inducing parameter variations

To introduce asymmetry in predation in the model, I strengthened the predator functional response to the competing prey (prey 2 in the experiments) by making its catches more frequent than the focal prey (prey 1 in the experiments). The change in the focal prey's final density compared to the baseline scenario, caused by a change in the competing prey dynamics (apparent competition effect), was expected to be stronger because more catches should have sustained a larger population of predators (Courchamp, Langlais and Sugihara, 2000; Roemer, Donlan and Courchamp, 2002). Yet, in the experiments, the focal prey final density actually increased with a stronger functional response to the competing prey. Indeed, both calibration and sensitivity analysis experiments showed that the model was very sensitive to the catch probability parameter, in the sense that increasing its value caused frequent extinction of the predator due to rapid prey depletion by over-predation (a predation rate that the focal prey population cannot withstand in the long term). Even when the catch probability parameter value was only increased for the competing prey, over-predation subsequently decreased the predator density and offered a predation relief on the focal prey, alleviating the AC effect. In this simulation experiment, both prey populations had the same growth rate, but the catch rate of the competing prey was greater than or equal to the focal prey, so the focal prey should have the highest growth-rate-to-catch-rate ratio and is thus expected to be the superior competitor (the one with the highest final density) according to the P* rule (Holt, Grover and Tilman, 1994). This rule held here. It is perhaps counter intuitive given previous research in terms of introduction of another prey species that is more easily caught than the resident prey, expected to result in an overall increase of predation and decline in the resident prey species (DeCesare *et al.*, 2010). But, in the field, two prey populations that only differ by the functional response of their shared predator would very unlikely have the same growth rate (or the same other characteristics, as in the simulations), and the population that is more subject to predation will most likely have evolved a higher growth rate to be able to withstand predation (Sinclair *et al.*, 1998), or differentiated niche to escape predation (Holt, 1977; Bonsall and Hassell, 2000). Yet, the impact of asymmetry in the catch probability in isolation of other characteristics had not been explored in modelling studies before. An equivalent of my experiment on catch probability asymmetry would be, e.g., to put a naïve subset and a predator-trained subset of the same prey species at similar densities in contact with a predator and measure apparent competition effect on the trained subset in the short term, before the naïve subset learns. In conclusion, these simulation results are consistent with AC theory, and the predator population was very sensitive to the strength of the functional response regarding extinction risk, but the effect on the intensity of AC on the focal species was positive and rather weak compared to other sources of asymmetry in predation.

In theory, a stronger (weaker) numerical response to the competing prey than to the focal prey species is expected to increase (decrease) the AC effect on the focal prey due to a higher (lower) number of predators produced by consuming the competing prey. It was the case in the experiment, until increasing further the resource per catch caused the predator density to be too high and deplete the prey until predator extinction by prey scarcity. Interestingly, varying the asymmetry in predator's numerical response resulted in symmetrical apparent competition between the two preys. Indeed, varying the resources per catch allowed a higher or lower predator survival and reproduction rate with the same catch rate on both preys; it did not change anything intrinsic to the prey, so the prey populations ended up undertaking the same predation pressure. The growth rate and attack rate being the same for both preys, the P* rule predicts no superior competitor; this was confirmed by the simulations. These results are consistent with a study of the consequences of bear kleptoparasitism on protected lynxes in a Slovenian national park (Krofel and Jerina, 2016). Lynxes feed on a kill for several consecutive days, but the introduction of protected bears in lynx hunting ranges greatly increase usurpation of kills (kleptoparasitism) by bear scavengers. This could be translated as a decrease in the prey resources per catch for lynx. Facing this significant energy loss, lynx compensate by strongly increasing hunting, with a subsequent drop on the prey populations and a feedback loop on energy loss. If the situation continues, lynx populations might severely decline due to a combination of prey scarcity and energy loss due to a decrease in the resources they acquire per catch. This example is another demonstration of the model accuracy in terms of theory and actual cases of AC.

The model's strong sensitivity to the catch probability could thus be mitigated by more stochasticity in the amount of resources the predator absorbs when catching a prey. For now, a catch systematically provides Υ_i resources to the predator, while prey's resource absorption is more stochastic (see section 3.2.3.2). If the predator's resource per catch was also sampled randomly between 0 and Υ_i, the increase in predator population density would be less drastic and preys' depletion less likely. This could model predators that do not always consume their catch entirely, by behaviour or because of disturbances (scavengers, enemy approaching, kleptoparasitism, etc…) or simply that the quality of the catch can vary (this option is implemented but was not tested here).

A primary prey with a higher growth rate sustaining a higher density of predators and decreasing the density of secondary prey that grows slower is the canonical case of asymmetrical apparent competition (Courchamp, Langlais and Sugihara, 2000; Roemer, Donlan and Courchamp, 2002; Courchamp, Woodroffe and Roemer, 2003; DeCesare *et al.*, 2010; Wittmer *et al.*, 2013; Ng'weno *et al.*, 2019). In the simulations, varying the fertility parameter value of the competing prey impacted its intrinsic growth rate and therefore its capacity to withstand predation compared to the focal prey. The results met the expectations as the presence of a prey that reproduced faster (slower) than the focal prey resulted in a stronger (weaker) AC competition effect on the focal prey. Since the catch probability – the equivalent of the attack rate in my model – was fixed in this experiment, the superior prey was the one with the highest growth rate, once again the P* rule was confirmed. The model sensitivity to asymmetry in growth rate was weaker than other sources of asymmetry. This is most likely because fertility indirectly impacts growth as the animals still need to have sufficient resources to pass the reproduction trial. Varying the asymmetry in the cost of reproduction might have had a stronger, more direct effect on the growth rate. A surprising result was that, although the prey population with a higher growth rate was higher in number and therefore more frequently encountered by predators than the focal prey population, the catch rate ranges (at the end of a moving and feeding sequence) of both preys overlapped regardless of the value of λ_2 (Figure 13). It would be whereas expected that this situation translates into a stronger realised catch rate on the most abundant prey population. My explanation is that, if we could see the evolution of the catch rate along the timesteps between two survival and reproduction trial (to limit computational time I assessed the population dynamics after reproduction trials and not in between), the catch rate of the most abundant prey would be higher in the first timesteps, because it would temporarily be more frequently encountered than those of the declining prey population. But as members of the most often encountered prey population are caught, the members of the declining prey population are increasingly more likely to be taken, and by the 10th timestep when come the trials, the catch rates might have evened out to the value corresponding to the predator density.

Finally, asymmetry in predation was generated by changing the carrying capacity of the competing prey, but not the focal prey. In the simulations, this asymmetry was generated by increasing (decreasing) the maximum resource consumption or the resource abundance of the competing prey only. In a ODE model based on two real-world cases of apparent competition involving caribous (competition with deer mediated by cougars, with moose mediated by wolf), Serrouya *et al.* (2015) predicted that increasing the carrying capacity of the alternate prey species but not of the caribou population would increase the apparent competition effect on the caribou population. My results verified this in the parameter range that did not cause any extinctions. Yet, in this range, neither the growth rate nor the catch rate differed between prey species, so the P* rule predicts no superior prey competitor. It is an interesting contradiction, because in AC's fundamental paper, Holt (1977) suggests that, in a prey species ensemble, the persistence of a given prey is independent of its own carrying capacity but might strongly depend of that of the other prey populations. But, in Holt's paper introducing the P* rule (Holt, Grover and Tilman, 1994), there is no mention of the carrying capacity as a factor influencing the persistence of a given species, probably because there is no assumption about the shape of population growth being logistic (no appearance of carrying capacity in the mathematical reasoning). The agent-based nature thus helped showing that the asymmetry in prey resource availability might also be an important argument in predicting the outcome of apparent competition.

3.5.3. Accounting for oscillations and cycles

Oscillations in density make populations more sensitive to stochastic environmental or human-induced perturbations, especially when they oscillate close to low densities, where Allee effects (negative growth rate at low densities) can lead to extinction (Stephens and Sutherland, 1999). In AC field studies, predator-mediated Allee effect has been shown to cause concerning declines in secondary prey species, including Caribou in British Columbia (Wittmer, Sinclair and McLellan, 2005; Wittmer *et al.*, 2013) and hartebeest in a Kenyan reserve (Ng'weno *et al.*, 2019). It might then be interesting to managers that increasing the asymmetry in predator numerical response and preys' carrying capacity most strongly impacted the amplitude of the oscillations in the focal prey species density. Changing the asymmetry in predator functional response and prey fertility once again had a weaker but noticeable impact on oscillation amplitude. A study of AC system exhibiting cycles with an adaptation of Holling's (1959) disk equation (deterministic mathematical model) showed that, in a system with two self-limiting prey and a prey-limited predator, cycling should weaken AC when "predator's per capita growth rate is a concave function of prey density" (Abrams, Holt and Roth, 1998). In the experiments in which varying the asymmetry in predation induced cycles (all but the fertility experiment), the only one in which larger cycles were associated to a lower AC effect on the focal prey than in the baseline (no cycling) scenario was the functional response experiment. In the other experiments concerned, larger cycles were coupled with a stronger AC effect on the focal prey than the baseline scenario. Again, the authors' first assumption is met by construction and the possibly unmet assumption is the predator numerical response, which emergent shape does not correspond to the usual relationships assumed in mathematical models (Figure 20). Consequently, the conclusions from Abrams, Holt and Roth (1998) might not apply to my agent-based model. However, a modelling study, inspired by hen harrier-mediated apparent competition between vole and grouse, argues otherwise (Barraquand *et al.*, 2015). The authors showed that, in their mathematical model of AC between self-limited prey species and a prey-limited predator with constant, linear, or logistic numerical responses, higher variability in the competing prey species strengthened the detrimental effect of AC on the focal prey. Thus, Abrams, Holt and Roth (1998) did not accurately predict the outcome of this case of AC but my agent-based model did, with no assumptions on the shape of the numerical and functional responses.

3.5.4. Importance of the shape of predator's functional response

When discussing the correspondence between my model and the classical assumptions of mathematical models in the literature, the shape of the predator's functional and numerical response was the main point of argument. Indeed, the shapes obtained in the model did not correspond to any usual numerical response in predator prey dynamics in the literature I reviewed (Figure 20). These shapes could relate to a lag in the change in the predator catch rate and growth rate following a change in the prey populations densities (e.g., catch rate increases linearly with decreasing prey densities, decreases with prey scarcity and then stagnates to low values when prey population are increasing again) but there was no mention of this in studies modelling, even explicitly, such a time lag (Barraquand *et al.*, 2015; Serrouya *et al.*, 2015). Modelling the functional and numerical responses as emerging from lower-level predator-prey interaction therefore put in perspective the way these capital characteristics has been assumed in mathematical models.

3.5.5. Potential effects of interaction between sources of asymmetry

Testing the impact of the interaction of these parameters intensifying AC between prey species would have been too computationally demanding, but some of these impacts can be inferred from model results. The effects are most likely cumulative when they induce the same AC effect on preys. For example, a competing prey that has both a higher catch probability and induces a stronger predator numerical response than the focal prey will most likely exacerbate the risk of prey depletion and the predator extinction. I also suspect that these sources of asymmetry can compensate for each other when inducing opposite effects. If the competing prey is less likely to be caught but has a higher carrying capacity than the focal prey, there might be a balance between the effects. Indeed, these sources of asymmetry in apparent competition rarely vary independently in nature. Over evolutionary time scales, prey in AC systems will most likely evolve higher growth rates to compensate for a high predation rate (Holt, 1977; Sinclair *et al.*, 1998; Chesson, 2000), reduce their catch probability by isolating from the competing prey through niche differentiation (Schmitz and Booth, 1997; Chesson, 2000; Holt and Bonsall, 2017), predators adapt their functional response for the prey with which they have the most optimal energy to conversion into offspring trade-off (Schmitz and Booth, 1997; McPeek, 2019).

3.5.6. Impact for conservation

However, unlike natural processes over large evolutionary time scales, biodiversity conservation measures and species management can alter either one of these sources of asymmetry independently over very short time scales. Unsurprisingly, this study confirms that biodiversity managers should be extra cautious when implementing policies that impact predator numerical response, such as diversionary feeding (Thirgood *et al.*, 2000; Krofel and Jerina, 2016). Policies directly impacting prey carrying capacities, including supplementary feeding or reduction of available resources, providing, or removing refuges from predation, should also be implemented with a full consideration of the possible indirect effect on other members of the trophic system. The same goes for introducing a predator that has a strong asymmetry in the efficiency with which it converts each prey catch into new offspring, or introducing a prey that exploits its resources more efficiently than the focal prey (Courchamp, Langlais and Sugihara, 1999, 2000; Roemer, Donlan and Courchamp, 2002; Courchamp, Woodroffe and Roemer, 2003; DeCesare *et al.*, 2010). These results also suggest that measures impacting fertility (like offspring control such as egg oiling) or promoting offspring survival (Pollard, 2018) could have less impact in systems of AC than the other interventions evoked here. Similarly, introducing a prey with a different average number of offspring might be less concerning for the managed species than the other characteristics tested here.

Overall, the predictions of apparent competition theory according to mathematical modelling and comparison to field cases were well-supported across the simulations, with the notable exception of the P* rule in the resources' abundance experiment and an open debate on the role of density cycles on the strength of apparent competition. Also, an important advance is that agent-based approach allows the modelling of apparent competition without assuming the shape of the functional and numerical responses, which have been proven to play a key role in dynamics. The sensitivity analysis also informs future users on the mechanisms requiring particular attention when predicting apparent competition outcomes. My model is therefore fit for purpose, meaning that it can serve as an effective framework for addressing major questions in apparent competition, and for the conservation of species involved in it, using an agent-based approach. Now that we are confident in the fact that the model can simulate the emergence of apparent competition in its fundamental version, the next step is to show how the model can be used to evaluate management strategies.

4. An agent-based tool to evaluate removal strategies for the conservation of species endangered by apparent competition

Abstract

In this chapter, I demonstrate how to use my Chapter 3 model to evaluate management strategies when a conserved population is involved in apparent competition with other species. I calibrate the model to a system in which a prey species of conservation interest is stable in presence of its predator but progressively goes extinct after the introduction of a more abundant, faster growing, alternate prey species through apparent competition. I then evaluate and compare the efficiency of three removal strategies for the conservation of the endangered prey population, while controlling for the persistence of the other species in the system. Strategies include (i) removal of predator only, (ii) removal of introduced prey species only, (iii) simultaneous removal of predator and introduced prey species, for which I explore different combinations of removal rates. All strategies successfully prevent the extinction of the endangered population, but some rate combinations of the simultaneous removal strategy guarantee a higher final density for the endangered species along with high densities of the alternate prey and predator populations and more stable dynamics. Comparing these results with previous studies of apparent competition management using mathematical models, I argue that the agent-based approach, especially through its time and spatially explicit nature, can make more realistic predictions on the outcome of conservation policies. All combinations of these removal strategies are now available in my model for evaluation by researchers or managers in other cases, and my method proposes to conserve the endangered population while considering the persistence of the other species in the system.

Résumé

Dans ce chapitre, j’utilise mon modèle du chapitre 3 pour évaluer des stratégies de gestion dans un cas de compétition apparente. Je calibre le modèle sur un système dans lequel une espèce de proie est stable en présence de son prédateur, mais s’éteint progressivement par compétition apparente après l'introduction d'une autre proie, plus abondante et à croissance plus rapide. Ensuite, j'évalue et compare l'efficacité de trois stratégies de contrôle pour la préservation de la proie en danger d’extinction, tout en surveillant la persistance des autres espèces dans le système. Les stratégies sont les suivantes : (i) réduction de la population de prédateurs, (ii) réduction de la population de la proie alternative et (iii) réduction simultanée des populations de prédateur et de proie alternative. Pour chacune d’elles, j'explore différentes combinaisons de taux de réduction. Toutes ces stratégies ont permis d'éviter la disparition de la population menacée, mais certaines combinaisons de taux dans la stratégie (iii) ont permis une densité finale plus satisfaisante pour l'espèce menacée, ainsi que des densités élevées pour l’autre proie et le prédateur, et une dynamique plus stable du système. En comparant ces résultats avec de précédentes études sur la gestion de la compétition apparente par des modèles mathématiques, je défends que l'approche individu-centrée, en particulier par sa nature temporellement et spatialement explicite, peut faire des prédictions plus réalistes sur le résultat des programmes de conservation. Toutes les combinaisons de ces stratégies de contrôle sont disponibles dans mon modèle pour évaluation par des chercheur·euses ou des gestionnaires dans de nouveaux cas, et ma méthode propose de préserver la population menacée tout en donnant de l’importance à la persistance des autres espèces dans le système.

4.1.Introduction

Apparent competition (AC) is an indirect negative interaction between individuals, populations, species, or entire functional groups, mediated through the action of one or more species of shared natural enemies (Holt, 1977; Holt and Bonsall, 2017). In predator-prey dynamics, AC is an indirect negative interaction between prey species that share one or more common predators. Most of the time, predator population size will be enhanced by an abundant primary prey species that is fit to withstand high levels of predation, thus increasing predation on rarer, less adapted secondary prey species (Sinclair *et al.*, 1998; DeCesare *et al.*, 2010; Holt and Bonsall, 2017). These indirect interactions are known to play a key role in the shape of trophic communities, in species exclusion, and to be a driver of niche differentiation (Bonsall and Hassell, 1997; Chesson, 2000; Chesson and Kuang, 2008; McPeek, 2019). Consequently, AC is an important mechanism to consider in the conservation of biodiversity.

Indeed, human intervention can very easily induce perturbations to AC systems over short periods of time, especially through species introduction, accidental or on purpose (Wittmer, Sinclair and McLellan, 2005; Wittmer *et al.*, 2007, 2013; DeCesare *et al.*, 2010; Krofel and Jerina, 2016). Even conservation measures can have adverse and unexpected effects due to AC, sometimes resulting in the decline of a species of conservation interest. An example is an insular case of introduced cat-mediated apparent competition between rodents and endangered endemic bird species, where both cats and rodent prey on the bird species. Rodent predation by cats reduced the overall predation pressure on the birds but at the same time, the abundant rodent population sustained an ever-increasing population of cats, causing biodiversity and health problems. The control of cat population caused a strong and sudden increase in the rodent population resulting in a higher predation pressure on the bird species than before cat control implementation (Courchamp, Langlais and Sugihara, 1999). Another example is the establishment of a natural reserve for protected huemuls in Patagonia. Huemul population was declining because of apparent competition with abundant introduced sheep which sustained a higher number of their shared predator: pumas. During the first years after displacing all sheep stock to establish the reserve, puma's predation on huemul strongly increased due to prey switching, causing a concerning decline in the protected population (Wittmer, Elbroch and Marshall, 2013; Wittmer *et al.*, 2013). When a managed species interacts somehow with human activities, such unexpected effects can escalate to conservation conflicts between human stakeholders (Courchamp, Woodroffe and Roemer, 2003; Ng'weno *et al.*, 2019). For example, a conflict arose between game-grouse managers and hen harrier's conservationists in the UK because of the dynamics of a hen harrier-mediated apparent competition between voles and red grouse. Game hunters want to protect grouse from predation by removing hen harriers while conservationists want the hen harrier protection policy in place to be strictly respected. To avoid grouse predation by hen harriers, game keepers used diversionary feeding, offering voles to the raptor. Instead, this method increased hen harrier population and, consequently predation on grouse, leading game keepers to reconsider removal methods (Thirgood *et al.*, 2000; Redpath and Thirgood, 2009; Barraquand *et al.*, 2015). To avoid these kinds of issues, AC must be better integrated to management strategy evaluation to make more effective policies.

Simulation modelling is a powerful tool for providing insights on the mechanisms at stake in apparent competition systems (Holt, 1977; Holt and Lawton, 1993; Holt, Grover and Tilman, 1994; Abrams, 1998; Abrams, Holt and Roth, 1998; Barraquand *et al.*, 2015; Holt and Bonsall, 2017; McPeek, 2019) and it has served as a decision-helping tool in conservation policy making (Courchamp, Langlais and Sugihara, 1999, 2000; Roemer, Donlan and Courchamp, 2002; Courchamp, Woodroffe and Roemer, 2003; Serrouya *et al.*, 2015). However, an increasing level of complexity is required to further understand and more accurately predict the multiple sources of AC and their consequences on animal communities. More specifically, the role of population structure (Bonsall and Hassell, 2000; Mouquet *et al.*, 2005), spatial dynamics (Schmitz and Booth, 1997; Holt and Barfield, 2003; Forrester and Steele, 2004; Orrock, Holt and Baskett, 2010; Ng'weno *et al.*, 2019), temporal dynamics (Holt and Barfield, 2003; Barraquand *et al.*, 2015; Serrouya *et al.*, 2015; Smith and Hall, 2016), or active behaviours (Schmitz and Booth, 1997; Bonsall and Hassell, 2000) have been identified as needing further research (Holt and Bonsall, 2017). Despite the great advances in theory it permitted, the classical approach using mathematical modelling is limited when incorporating the aforementioned mechanisms, especially simultaneously. Alternatively, agent-based models (ABMs) can be used to better integrate this complexity in modelling. ABMs are often more appropriate for addressing theoretical questions at small scales, with finite and small populations, non-equilibrium dynamics, spatial and temporal complexity and flexibility in individual behaviours (Uchmański and Grimm, 1996; DeAngelis and Grimm, 2014; Stillman *et al.*, 2015) and should therefore be more widely applied to AC systems. Indeed, in these systems, the landscape characteristics, foraging behaviours, and local interactions between animals greatly influence the intensity of indirect competition. However, if ABMs are increasingly widespread in ecology (Schmitz and Booth, 1997; Bocedi *et al.*, 2014, 2021; DeAngelis and Grimm, 2014; Ayllón *et al.*, 2016; Railsback, Ayllón and Harvey, 2021), they are more scarcely used in conservation

(Bousquet and Le Page, 2004; Duthie *et al.*, 2018; Railsback, Ayllón and Harvey, 2021) and were, until now, non-existent in apparent competition.

Chapter 3 of this thesis introduced and demonstrated the accurate functioning of a spatially, timely explicit ABM for predator-prey dynamics under apparent competition. In the present study, I demonstrate how to use this model to evaluate alternative management strategies to conserve a species endangered by AC. The most widespread method to conserve such a species is by controlling the other species' densities (Courchamp, Langlais and Sugihara, 1999, 2000; Roemer, Donlan and Courchamp, 2002; DeCesare *et al.*, 2010; Serrouya *et al.*, 2015). In the classical case of a prey species endangered by the presence of another, more abundant, primary prey species that better withstands predation, Wittmer *et al.* (2013) identified the three most common control strategies to be (i) the control of the predator population, (ii) the control of the primary prey, and (iii) the simultaneous control of the primary prey and predator populations. In this study, the strategy (i) was identified as effective to protect endangered bird species (Côté and Sutherland, 1997) until predator control stops or weakens and the high density of primary prey causes too strong a predation pressure on the endangered prey. Strategy (ii) was expected to have a detrimental effect on the endangered prey density in cases of high numbers of predators at the time of implementation, as removal of the more abundant prey population could cause prey-switching and increase predation pressure instead. Finally, strategy (iii) is expected to be the safest, as it undermines both these effects. Any of these strategies being preferable than leaving the situation unmanaged. Most of these expectations were explored in a previous mathematical study on the case of golden eagle-mediated apparent competition between an abundant population of introduced feral pigs and an endangered endemic island fox population on the Californian Channel islands (Courchamp, Woodroffe and Roemer, 2003). This study will be ideal to confront results with.

Using my novel ABM, I will confront these predictions by evaluating the efficiency of each strategy on the intensity of AC on an endangered prey, compared to a null strategy of no management intervention, in a canonical model case of apparent competition. The spatially explicit, bottom-up approach of my ABM will relax key assumptions about predation in mathematical model and challenge the robustness of their predictions when modelling AC more mechanistically. In the spirit of avoiding the rise of conservation conflict, I will evaluate these strategies with a focus on the endangered prey dynamics, while controlling for the persistence and the stability of the other species in the AC system.

4.2.Methods

4.2.1.Model

The model description follows a condensed version of the ODD (Overview, Design concepts, Details) protocol (Grimm *et al.*, 2006, 2010, 2020). All model details can be found in the section 3.2 of the previous chapter. Every detail present in Chapter 3 but not mentioned here was not modified for this chapter's simulations.

4.2.1.1. Overview

4.2.1.1.1. Purpose

The purpose of the model is to simulate trophic interactions between an abundant prey population, an endangered prey population and a shared predator population when a removal control policy is applied to the abundant population, to the predator, or both simultaneously. The aim is to anticipate these policies' potential adverse effects resulting from apparent competition between prey species mediated by predation. The ABM approach makes it possible for this model to account for important aspects of population dynamics that cannot be included simultaneously in deterministic models, such as stochastic spatial heterogeneity in animal positions, intrinsic uncertainty, or non-equilibrium dynamics. Moreover, the predator numerical and functional responses and the prey catch rates are emergent properties of the model, allowing to relax the assumptions made in mathematical models for these mechanisms. This work will evaluate the propensity of removal strategies to conserve the endangered prey species, without putting the other species at risk of extinction.

4.2.1.1.2. Entities, state variables and scales

Landscape

All animals are simulated on a square grid lattice landscape of size S x S cells. Each cell is characterised by an x and a y location, a reference number unique to the cell, a certain amount of resources of two different kinds present on the cell, a maximum amount of resources that the cell can hold, the density of each animal present, and the count of catches of each prey types during a timestep.

Animals

Animals move, and interact with resources and other animals, on landscape cells. They are characterised by an x and a y position on the grid, the associated cell number, a type (here prey 1, prey 2 and predator), a dead or alive status, an age, a resource stock, and a number of offspring produced. The movement range (in fraction of S), satiation level, cost for maintenance and for reproduction (all in resource units), diet, average expected number of offspring produced (fertility), and time of introduction depend on the population to which they belong.

Animals – preys

Prey entities are modelled as a specific type of animal, distinct in the way that they harvest resources. Prey absorb resources directly from the landscape cells. Each prey population has specific values for their animal characteristics and feed on a unique resource (i.e., there is no competition for resources between prey populations).

Animals – predators

Predators are modelled as a specific type of animal entity, distinct in the way that they acquire resources. They gain resources by capturing prey that occupy a shared landscape cell. Predators have additional characteristics that distinguish them from other animal entities. These characteristics are a conversion rate of a prey captured into resource units for each prey type, and a probability of catch for each prey type. Predators feed on both prey species with no particular preference.

Spatial and temporal scales

Timesteps and spatial scale are abstract in the model, but in this study, a single timestep could be conceptualised as the equivalent of a month, and a single grid cell could be conceptualised as equivalent to one hectare.

4.2.1.1.3. Process overview and scheduling

In all the following processes involving animals in a timestep, prey populations act first, in order of prey type, followed by the predator population, provided that the current timestep is passed their respective introduction time. A timestep begins with animals moving, which updates the position of each animal on the landscape and of each animal type's densities on the cells. Next, prey feed and predators hunt, which updates the animals' individual resource stock, preys' status (dead or alive) and prey type's densities on cells. Every 10 timesteps, the following processes occur: a proportion Q_i of animals of population are removed (if applicable); all living animals undergo a survival trial to update their dead or alive status; the survivors then undergo a reproduction trial to update the animals' number of offspring produced. The animal tables are updated, accounting for deaths, increasing survivors age by 1, and introducing offspring as new individuals. Lastly, the animal type's density in landscape cells is updated accordingly at the end of the timestep. A timestep then finishes by saving the density of resources, prey, catches and predator density on the landscape, appending to a results table. Every 10 timesteps, the landscape cells resources are replenished to their maximum before starting a new timestep cycle (Figure 21).

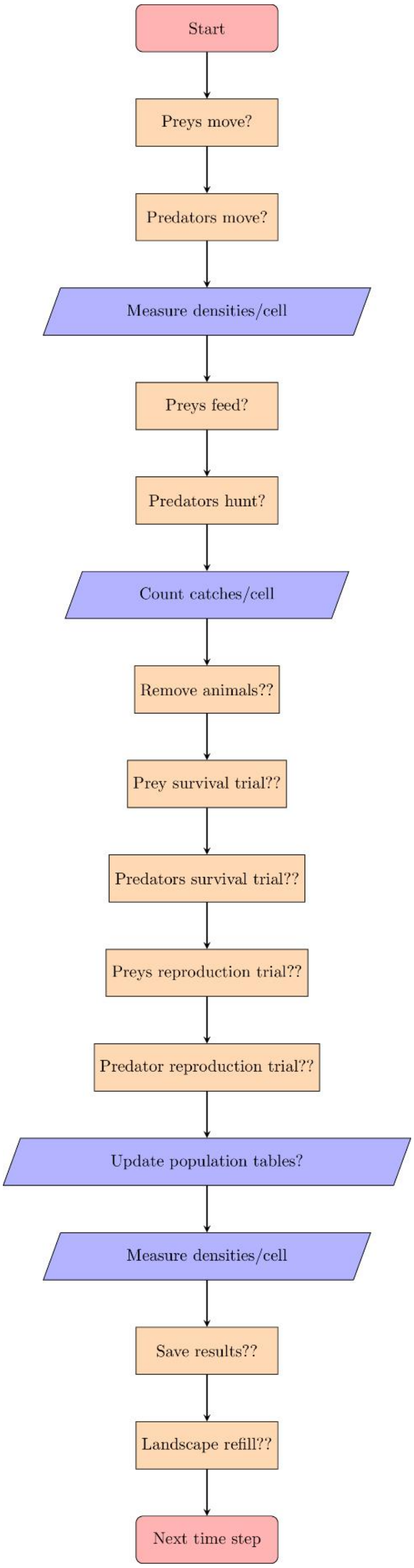

Figure 21. General flowchart of a timestep in the model. Boxes finishing with a '?' are realised only if the timestep is superior to the time of introduction of the given species. Boxes finishing with a '??' are realised only if, in addition, the timestep is a multiple of f_{surv}. Species undergo

removal if their population was entitled to it and if the time is passed the policy's starting timestep.

4.2.1.2. Design concepts

4.2.1.2.1. Stochasticity

Species removal

Species removal is carried out after randomly shuffling the species population table to ensure spatial and inter-individual stochasticity in removal.

4.2.1.2.2. Observation

The observed variables are the density of each population on the landscape and the number of successful catches by predators in each prey population. In this study, these variables are measured after each survival and reproduction trial. They make it possible to compute other measures such as populations' catch rate, fluctuation amplitude, or extinction rate.

4.2.1.3. Details

4.2.1.3.1. Initialisation

At initialisation, a table containing the animal population densities and catch count is constructed. Resources are set to their respective maximums on each cell, and animals' positions are distributed at random with an empty resource stock, alive status (DoA = 1), 0 offspring and age 0. Structures are set up in timestep 0 and life events processes start on the next timestep. The endangered prey (prey type 2) and predator populations are introduced at timestep 0 at their pseudo-equilibrium densities in the absence of a third, faster growing, population of prey (prey type 1). After 300 timesteps (30 generations) of endangered prey - predator dynamics, the alternate prey species is introduced. After 70 generations, the removal policy is initiated.

4.2.1.3.2. Sub models

Species removal

If the given species is managed, meaning that some individuals can be removed from the population for conservation purposes, and if the simulation timestep exceeds the timestep of removal implementation, the removal quota/rate Q_i is computed according to the policy characteristics. Next, the population table is shuffled and parsed; if the randomly chosen animal is not already dead, then its dead or alive status is set to 0. The process is repeated until the quota has been attained or that there are no living animals remaining (Figure 22). Removal occurs after the moving and feeding sequence and at the same frequency as survival and reproduction trials.

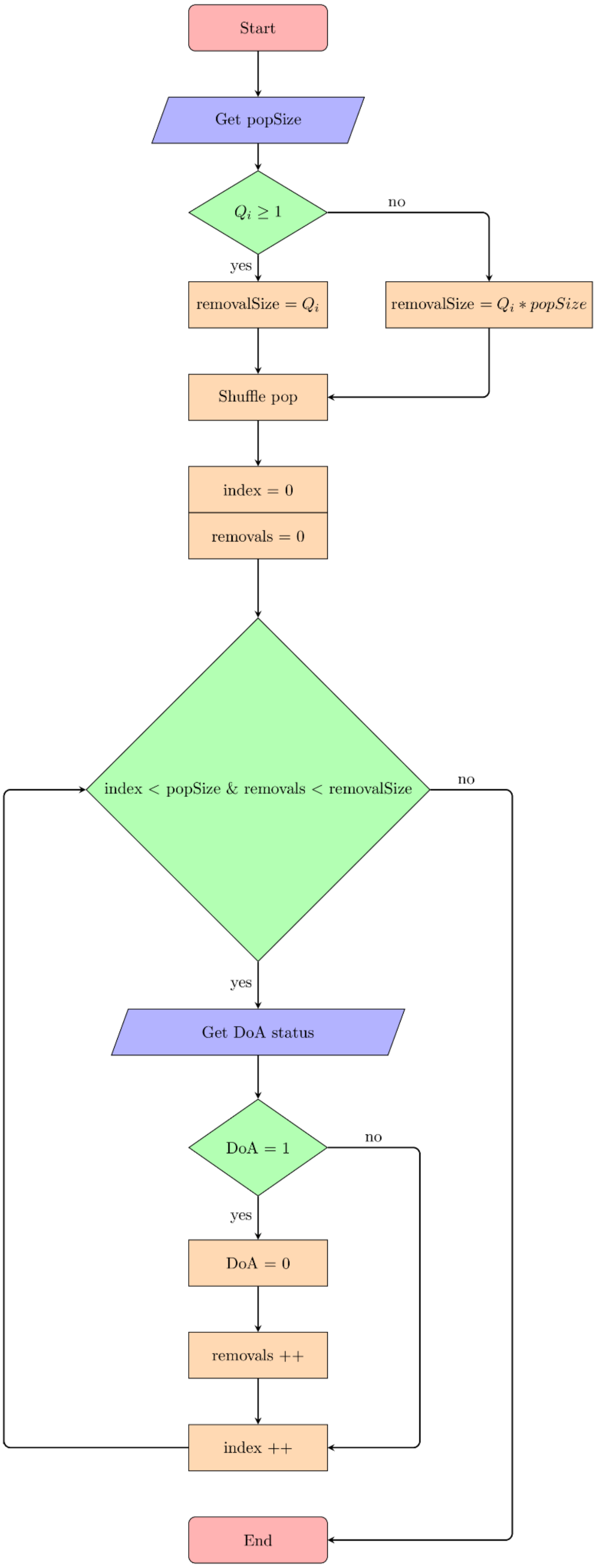

Figure 22. Flowchart of the removal function.

4.2.2. Calibration

4.2.2.1. Model case

I calibrated the model to a canonical case of apparent competition, where a resident prey species and its predator exhibit stable dynamics, but the introduction of another prey species with a higher growth rate (i.e., that better withstands predation) slowly excludes the resident species by sustaining a higher predator population, thereby increasing predation pressure on the resident species beyond the level it can withstand (Bonsall and Hassell, 2000; Courchamp, Langlais and Sugihara, 2000; DeCesare *et al.*, 2010; Serrouya *et al.*, 2015).

4.2.2.2. Assumptions and parameter setting

I assumed the predator to be a generalist, meaning that the predator feeds on both types of prey. I also assumed that predators had no preference for prey of either population. This was enacted by shuffling the vector of prey available for predation on a cell before undergoing the capture trials, and setting the prey catch probabilities to the same values. This ensured that predation pressure variations would only be linked to the emergent position and abundance of the prey. I assumed a relatively high growth rate for the primary prey (prey 1) in comparison to the resident, endangered prey (prey 2). Therefore, I have made the primary prey more efficient in converting resources into offspring by setting its reproduction cost to a lower level than the endangered prey. I assumed the same level of available resources for each prey species and set the levels to a high value, allowing prey species to stabilise at high pseudo-carrying capacities in absence of predation. Consequently, prey species dynamics were much more strongly limited by predation than by resource availability. I assumed the prey to be of equivalent size and abilities such that the predator was as efficient in acquiring resources from both prey species. Therefore, I set the two preys' maximum consumption, maintenance cost, and resources per catch to the same values.

4.2.3. Parameter exploration

First, I set the endangered prey parameters to the values in Table 5 and simultaneously varied this prey's maintenance cost μ_2 (setting the reproduction cost ρ_2 to the same value) and its catch probability p^{catch}_2 across a wide range of values before simulating the dynamics in the presence of the predator only. I selected parameter values for which the prey and predator populations stabilised to the highest densities with the lowest oscillations amplitude and no risk of extinction ($\mu_2 = \rho_2 = 40$ resources units and $p^{catch}_2 = 0.04$). Next, I varied the ratio between the primary and the endangered prey reproduction costs (ratio <

1, such that primary prey had a higher growth rate) and simulated the dynamics in the presence of both the predator and primary prey populations. I selected parameter values that resulted in the primary prey slowly but consistently excluding the endangered prey by maintaining a higher density of predator, with no risk of extinction for primary prey or predator populations ($\rho_1 = 25$ resources units, Figure 23). I choose this parameter set as the null strategy, i.e., no management intervention.

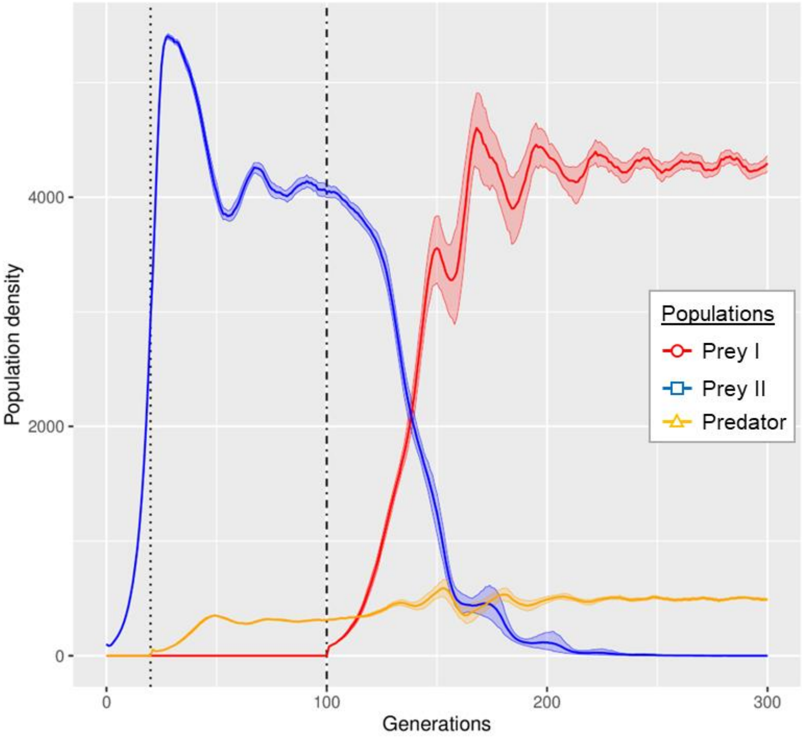

Figure 23. Evolution of the three species mean densities along generations with no management intervention. The coloured ribbons are the bootstrapped 95% confidence intervals around the means. The dotted line is the time of introduction of the predator population, the dot and dashed is the primary prey's.

4.2.4. Management scenario evaluation

4.2.4.1. Experimental plan

To evaluate the efficiency of the 4 different management strategies, I varied the primary prey (Q_1) and the predator culling rates (Q_P) within a range of 0 to 0.25 by 0.05 increments and simulated the dynamics over 200 generations in 50 replicates for every removal rate parameter value combination (removal rates above 0.25 caused consistent extinction of either the predator or the primary prey populations in preliminary simulations). A combination of both rates at zero corresponded to the null strategy, or no intervention whatsoever. A combination with a Q_1 (Q_P) of 0 corresponded to a predator (primary prey) removal only policy. Any combination with both Q_1 and $Q_P > 0$ corresponded to a simultaneous removal of primary prey and predator policy.

4.2.4.2. Simulations

The endangered prey and predator populations were introduced at timestep 0 at their densities of pseudo-equilibrium in absence of a second prey population (i.e., their densities just before the introduction of the primary prey in the calibration experiment, Figure 23). After 30 generations of burn-in, 100 animals of the primary prey population were introduced. After 70 generations, the endangered prey population was at very low densities, therefore needing management. The removal policy was implemented from the 100th generation and ran for another 100 generations, until the end of simulation (200 generations in total). All simulations were run with the model version v0.6.2, available for consultation at this link. The analyses were run on R (v4.2.1; R core team (2022)).

4.2.4.3. Measures

To evaluate the propensity of each strategy to conserve the endangered prey, I measured the final density of each species as the average density over the last 50 generations. Over the same period, I measured the difference between maximal and minimal densities to estimate the amplitude of the oscillations, if present. This approach avoided the artifact of estimating a mean final density over 50 generations which did not exactly cover a full multiple of a complete cycle. The extinction frequency was also assessed, calculated as the number of extinction events over the 50 replicates. I considered a removal strategy to be efficient when it allowed the endangered prey population to reach densities comparable to those observed in absence of the primary prey, with low to null extinction risk, and a low amplitude of oscillations, while also ensuring the persistence of the other species in the system. Parameters were set to the values in Table 5.

Table 5. Parameters table.

Class	Object	Name	Symbol	Value	Unit
Landscape		Size of landscape grid	S	25	cells
		Max resources of type 1	K_1	400	resource units
		Max resources of type 2	K_2	400	resource units
Animal	Prey 1	initial density	N^0_1	100	animals
		move range		0.1	fraction of S
		max consumption	σ_1	10	resource units
		maintenance cost	μ_1	40	resource units
		reproduction cost	ρ_1	25	resource units
		fertility	λ_1	1	animals

		time of introduction	t_1	0	timesteps
	Prey 2	initial density	N^0_2	4,000	individuals
		move range		0.1	fraction of S
		max consumption	σ_2	10	resource units
		maintenance cost	μ_1	40	resource units
		reproduction cost	ρ_2	40	resource units
		fertility	λ_2	1	animals
		time of introduction	t_2	1,000	timesteps
	Predator	initial density	P^0	300	animals
		move range		0.1	fraction of S
		satiation	σ_P	100	resource units
		maintenance cost	μ_p	200	resource units
		reproduction cost	ρ_P	400	resource units
		fertility	λ_p	0.5	animals
		time of introduction	t_P	0	timesteps
		catch proba of prey 1	$p^{catch}{}_1$	0.04	-
		resources per prey 1	Υ_1	100	resource units
		catch proba of prey 2	$p^{catch}{}_2$	0.04	-
		resources per prey 2	Υ_2	100	resource units
Other		Simulation time	t_{max}	2,000	timesteps
		Freq. of survival trials	f_{surv}	10	timesteps
		Freq. of repr. trials	f_{repr}	10	timesteps
		Freq. of resource refill	f_{fill}	10	timesteps
Management	Prey 1	Removal rate	Q_1	0 – 0.25	fraction of $N_1(t)$
		Starting time	t_{R1}	1,000	timesteps
		Frequency	f_{R1}	10	timesteps
	Predator	Removal rate	Q_P	0 – 0.25	fraction of $P(t)$
		Starting time	t_{RP}	1,000	timesteps
		Frequency	f_{RP}	10	timesteps

4.3. Results of the alternative strategies evaluation

4.3.1. No removal

Given no intervention whatsoever, the endangered prey population (prey 2) went extinct in 90% of the replicates (Figure 24) or otherwise ended at a very low final density (35.56 animals on average, with a bootstrapped 95% confidence interval of [27.72 ; 44.92]; Figure 25). The mean oscillations amplitude in density in the replicates that did not end in an extinction was very low, with a minimum of 8.6 and a maximum of 129 animals (Figure 26). The other species in the system stabilised at high densities with no extinction risk (Figure 24 and Figure 25). Without intervention, the introduced primary prey species would then consistently replace and exclude the endangered resident prey by sustaining a higher density of predator than the endangered prey can withstand.

4.3.2. Predator removal only

The predator removal policy consistently removed the risk of endangered prey population extinction, even when the predator removal rate was low, reducing prey 2's extinction frequency down to 0 from a 10% predator removal rate (Figure 24). The endangered prey final density steadily increased with the predator removal rate (Figure 25), even to a higher final density than alone with the predator for high removal rates (5,415.31 [5,409.94 ; 5,426.81] with $Q_P = 0.25$ versus 4,061.44 [4,032.27 ; 4,091.94] when alone with the predator). The amplitude of oscillations in the endangered prey's final density slightly increased for $Q_P = 0.15$ and 0.20 (up to around an amplitude of 1,000 for around 3,000 animals) but decreased back down to low amplitudes for the higher removal rate (Figure 26) , most likely because decline caused in the predator density.

Predator removal had no effect on predator or prey 1 extinction frequencies, which stayed at 0, and only a weak effect on their final densities, until reaching $Q_P = 0.25$ which caused the predator final density to drop to a low value (88.54 animals on average) with a slight increase in their extinction frequency (from 0 to 2% of the replicates). This relieved predation pressure on both prey populations, even allowing the primary prey final densities to increase to higher densities than in absence of management (Figure 24 and Figure 25). The amplitude of oscillations in predator and prey 1 final densities followed the same trends as prey 2's (Figure 26).

4.3.3. Primary prey removal only

The primary prey removal policy saved the endangered prey from extinction by reducing the extinction frequency to 0 given a 5% removal rate (Figure 24). The endangered prey final density steadily increased with increasing removal rate, even to a higher density than alone with the predator for high values (more than 5,000 animals for $Q_1 = 0.25$, Figure 25). The amplitude of oscillations in the endangered prey density increased with increasing removal rates until $Q_1 = 0.15$ (between 1,000 and 2,000 amplitude for between 2,000 and 4,000 individuals), after which the amplitude decreased again (Figure 26), most likely because decline caused in the primary prey density.

Increasing the removal rate also increased the predator population extinction frequency, with a slow but steady decrease in their final population. The primary prey population's extinction frequency increased from $Q_1 >= 0.2$, and its mean final density strongly decreased with increasing removal rate values (Figure 24 and Figure 25). Predator and primary prey populations showed the same trend as prey 2 in the amplitude of density oscillations (Figure 26).

4.3.4. Primary prey and predator simultaneous removal

Simultaneous removal of both the primary prey and the predator made the endangered prey safe from extinction for every possible combination tested (Figure 24). For each given predator removal rate values, increasing the prey 1 removal rate resulted in a higher endangered prey final density. Similarly, for any fixed primary prey removal rate, increasing the predator removal rate resulted in a higher endangered prey final density (Figure 25). The amplitude of oscillations in endangered prey final density was higher for low predator and low prey 1 removal but decreased again when increasing either the primary prey or the predator removal rates. Interestingly, for primary prey removal rates $Q_1 < 0.2$, setting up a combined predator removal policy protected the predator population from going extinct (until $Q_P = 0.25$ where the extinction risk was high again).

The primary prey was not threatened with extinction in any combination except {$Q_1 = 0.25$; $Q_P = 0.05$}, where the reduction in growth rate caused by the removal policy prevented the primary prey from withstanding predation (Figure 24). In combinations ensuring no extinctions, the predator population density ended up around the value in absence of the primary prey (306.77 [302.48 ; 310.85] animals on average before the primary prey introduction). Overall, the primary prey final density benefited from a higher predator removal rate, but their density declined for $Q_1 > 0.15$. Several combinations of Q_1 and Q_P resulted in high densities for all species, with low oscillation amplitude and no extinction risk; an example is shown in Figure 27. Generally, a low amplitude was obtained with a higher predator removal rate, sometimes at the expense of the predator population declining to very low densities before taking hold again.

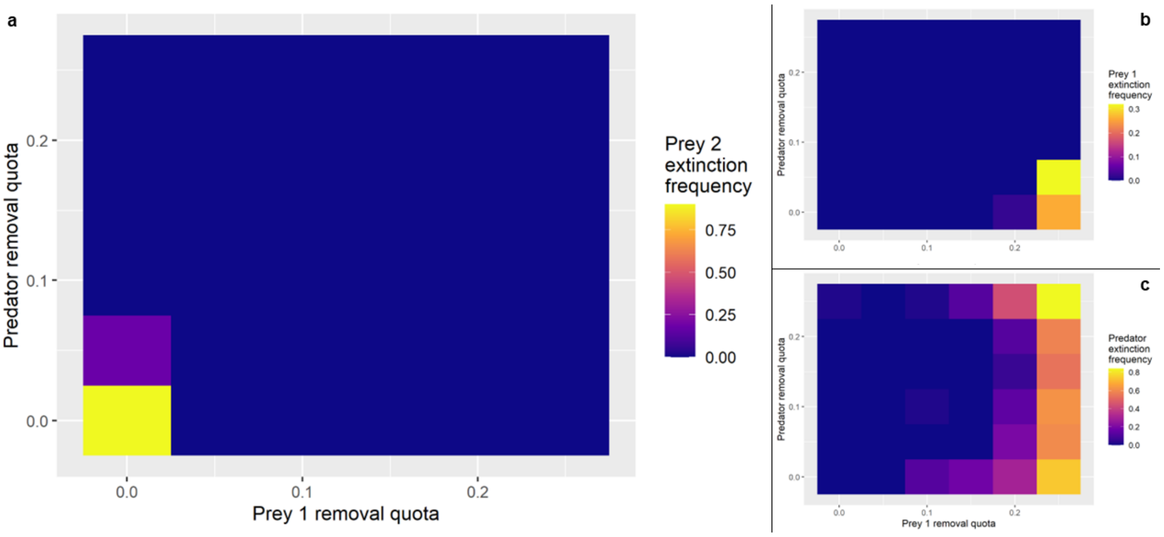

Figure 24. Heatmaps of the extinction frequency according to the different predator and primary prey (prey 1) removal rates for the endangered prey (prey 2, panel a), the primary prey (b) and the predator (c) populations. The lighter the colour, the highest the extinction risk. The colour range values are relative to each population results.

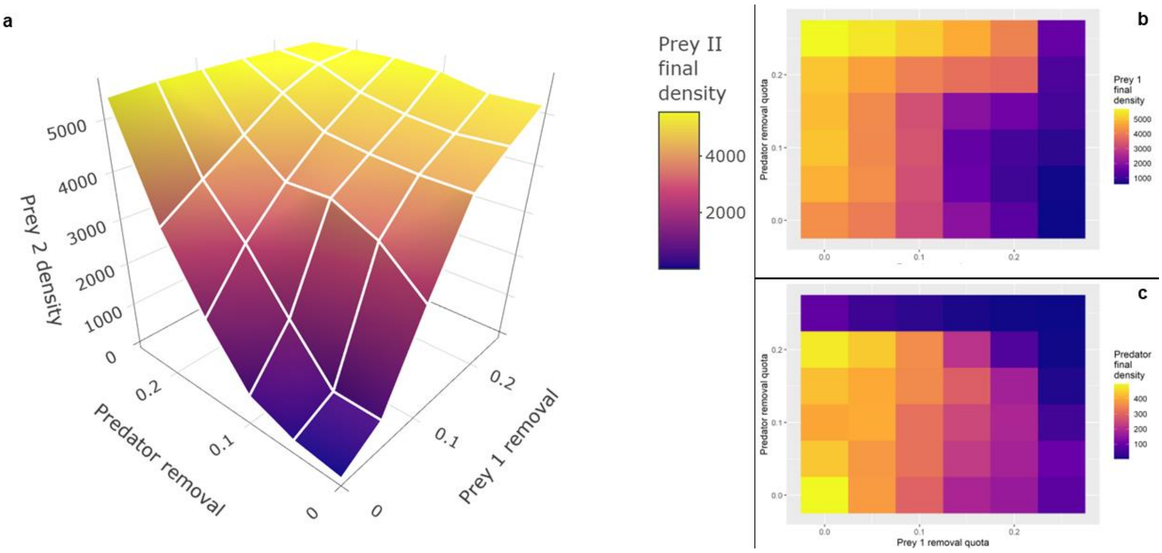

Figure 25. Mesh plot of the mean final density of the endangered secondary prey population (prey 2) according to predator and primary prey (prey 1) removal rates (a). Heatmaps of the mean final density according to predator and primary prey removal rates for the primary prey (b) and the predator (c) populations. The lighter the colour, the highest the density. The colour range values are relative to each population results.

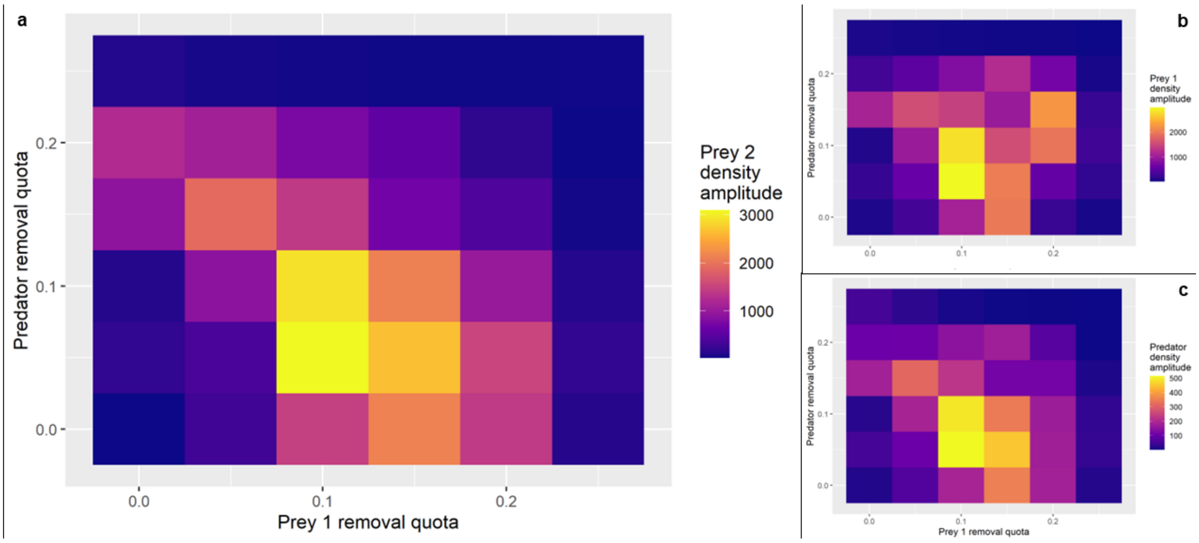

Figure 26. Heatmaps of the mean difference between the maximal and minimal final densities according to the predator and primary prey removal rates for the endangered prey (a), the primary prey (b) and the predator (c) populations. The lighter the colour, the larger the amplitude. The colour range values are relative to each population results.

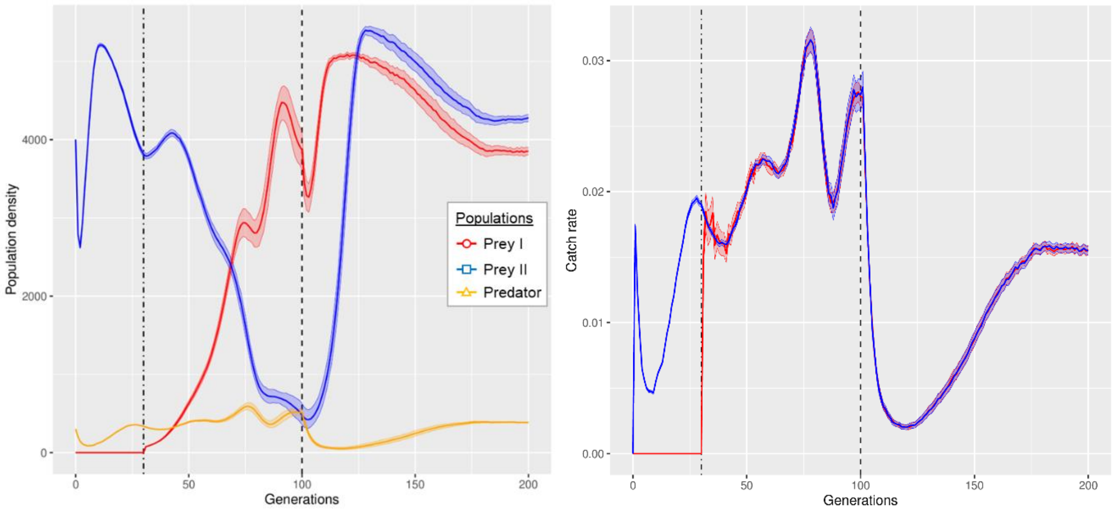

Figure 27. Evolution of the three species mean density (left) and of the number of catches relative to the density (right) along simulation timesteps with one of the removal policies that resulted in the highest final densities for the three species, with 0 extinction frequency and the least amplitude in oscillations (Q_1 = 0.1; Q_P = 0.2). The coloured ribbons are the bootstrapped 95% confidence intervals around the means. The dotted and dashed line is the time of introduction of the primary prey population. The dashed line is the time of first implementation of the removal policy. Note that even if there were no extinctions in the simulations, the predator population decreases close to very low number in the few generations preceding the time of implementation of the removal policy.

4.4.Discussion

My agent-based model simulated management in a case of apparent competition between an endangered prey species and a more abundant, faster growing, primary prey species mediated by a shared predator with no preference for either prey. I evaluated and compared the efficiency of three removal strategies in conserving the endangered prey population without threatening the other species in the system by testing several combinations of removal rates. The three strategies were (i) removal of predator only, (ii) removal of primary prey species only, (iii) simultaneous removal of predator and primary prey species. With no intervention, the endangered prey population consistently went extinct; all three strategies successfully reduced this extinction risk to zero, even with low removal rates. The endangered prey population density steadily increased with increasing removal rates in all strategies. The simultaneous removal of predator and primary prey resulted in higher endangered prey densities than removal of only one of the species. The amplitude of oscillations in the endangered prey density was maximised for combinations of low but positive predator and primary prey removal rates but decreased when the removal rates further increased. The primary prey species removal policy had a stronger effect in reducing both the predator and the primary prey densities, and therefore in increasing the endangered prey density, than the predator removal policy. For several combinations of the simultaneous removal of both the primary prey and the predator populations, the endangered prey and predator population ended up at levels similar to those in absence of the primary prey, with high densities for the primary prey and no extinction risk for any species.

The efficiency of the predator removal strategy in conserving the endangered prey species is consistent with previous works (Côté and Sutherland, 1997; Courchamp, Woodroffe and Roemer, 2003; Wittmer *et al.*, 2013). Indeed, the regular removal of part of the predator population instantaneously resulted in a decrease in prey catch rates, allowing both preys to increase in density. Nevertheless, these studies argue that the cessation of predation control must be planned carefully because allowing the predation population to increase again in presence of enhanced prey densities might lead to an even stronger apparent competition effect than before the policy implementation. In the face of this argument, the authors doubt about the long-term benefits of this strategy.

Using a mathematical model of a real-world case of golden eagle-mediated apparent competition between an abundant feral pig and an endangered island fox, Courchamp, Woodroffe and Roemer (2003) also showed that combining predator and primary prey removal resulted in better conservation outcomes for the endangered prey species.

Consistently, in my simulations, removal of the predator alone reduced the catch rate but did not markedly reduce the predator density; adding removal of the primary prey also decreased predator density, thus combining two positive effects on the endangered prey density.

An interesting point of disagreement with Courchamp, Woodroffe and Roemer (2003) is that the authors found removal of the feral pig prey population alone to consistently drive the endangered fox population to extinction. In this study's model, the decrease of the most abundant prey caused the share of the fox in the predator diet to increase, strengthening predation pressure on fox population. In my simulations, removing the primary prey instantaneously caused a strong reduction in the predator population, with a positive effect on the endangered prey density due to predation relief. On another hand, my result also confirms a previous study of a real-world wolf-mediated apparent competition between an abundant moose population and an endangered caribou population, in which the removal of part of the moose population resulted in a decline of the wolf population and an increase in caribou population (Serrouya *et al.*, 2015).

There could be several explanations for these contradictory results. First, in the model of Courchamp, Woodroffe and Roemer (2003), foxes are expected to go extinct after completely removing the feral pigs within 6 years. Is this extinction because the foxes could not withstand eagle predation in isolation with the eagle population? Roemer *et al.* (2001) showed foxes would indeed go extinct if they were the only prey of eagles. My model case was built such that the endangered prey could withstand predation in absence of the primary prey species (Bonsall and Hassell, 1997; Courchamp, Langlais and Sugihara, 2000; Wittmer, Sinclair and McLellan, 2005; DeCesare *et al.*, 2010). Additionally, previous studies showed that the eagle population cannot sustain only on foxes and can only settle in presence of an abundant feral pig population (Roemer *et al.*, 2001; Roemer, Donlan and Courchamp, 2002). This unsurprisingly means that the parameter set governing this eagle-fox-pig system is most likely different from my model case's, starting with the carrying capacity values. In Courchamp, Woodroffe and Roemer (2003) study, the carrying capacity of the endangered prey species (fox) was much lower than that of the abundant prey (feral pig). This might have limited fox population growth in addition to the increase of predation pressure when controlling the abundant prey population. Chapter 3 has shown that asymmetry in carrying capacities has a strong impact on the intensity of apparent competition in my model. I have tried to undermine this effect by setting a high ratio between the preys' consumption and the maximum amount of their resources per cell, resulting in high pseudo-carrying capacities for both species. Prey's dynamics were therefore more strongly limited by predation than by resource availability, allowing strong growth for both species at the densities of stabilisation in presence of the predator. This could be an explanation for these contradictory results.

Different assumptions regarding the predator functional responses modelling would unlikely explain this stronger predation on foxes. First because in Courchamp, Woodroffe and Roemer (2003), the conversion rates (equivalent of resources per catch in my model) of foxes and pigs were also set to the same values. Second, the attack rate was fixed but modulated by the instantaneous proportion of a given prey population relative to the total number of available preys and by the predator density, resulting in a catch rate function of all species' instantaneous densities. This modelling choice is similar to my model, in which the catch rate emerges from the interaction between a fixed catch probability, the proportion of a given prey relative to all the preys on a cell and the number of predators present on the cell (so by extension, from the emergent position and density of the animals). Nevertheless, my model assumes individual predator satiation, which is absent from Courchamp, Woodroffe and Roemer (2003) and might make predation less drastic in my simulations. Moreover, the most striking difference between our model cases was that Courchamp, Woodroffe and Roemer (2003), based on previous studies on the actual system (Roemer *et al.*, 2001; Roemer, Donlan and Courchamp, 2002), assumed a very strong predation preference for foxes. This model was parameterised with a bias for foxes in the eagle diet (more than 8 foxes captured for 1 pig captured), combined with a bias in the attack rates (more than 4 times higher for fox than for pigs). Interestingly, in the same system, Roemer *et al.* (2001) showed that these biases can have a strong impact on the outcome of apparent competition even in absence of management; a change of preference from 1 to 3 foxes for 1 pig resulted in a more rapidly declining fox population. On another hand, in the same system as Courchamp, Woodroffe and Roemer (2003), but in presence of a third prey species and without management, Roemer, Donlan and Courchamp (2002) showed that varying the fox parameters, including bias in diet and attack rate, by ± 10% had very little effect on the outcome of apparent competition. An equivalent of this model's attack rate parameter in my ABM would be the catch probability. In the present simulations, the preys' catch probabilities were set to the same values, resulting in the same catch rate for both prey species. To investigate this further, I repeated the experiment by setting an intrinsic preference of the predator for the endangered prey (predator preferentially prey upon the endangered prey if present, but still with the same catch probability for both prey types). This resulted in a slightly higher catch rate for the endangered prey, but the tendencies were the same as the experiment with no intrinsic preference, although with a slightly stronger extinction risk for the endangered prey at low removal rates. Thus, intrinsic preference alone might not suffice to explain the difference in our results. The sensitivity analysis in section 3.4.2.4 also showed that the asymmetry in catch probability between prey species had a positive impact on the intensity of apparent competition. Altogether, this suggests that the combination of a strong asymmetry in the fox attack rate with a strong bias for foxes in the eagle diet is an important factor explaining these contradictory results. Asymmetries in the predator diet and attack rates should then be carefully assessed before evaluating management strategies as it appears to be able to reverse the outcome of management.

Besides, the timesteps allowed between reproduction trials in my model might play an important role in reducing the bias in predation. After a reproduction trial, the primary prey population is expected to be more abundant than the endangered prey because it transforms resources into offspring more efficiently. Thus, the proportion of primary prey on a cell will often be larger than that of the endangered prey. Therefore, there should be more catch trials involving primary preys than endangered ones, and since satiation limits predators to one catch per timestep, they are more likely to be satiated on the primary prey, introducing an asymmetry in predation pressure to the benefit of the endangered prey. But as timesteps go passed from the reproduction trial, and as more members of the primary prey population are caught, the proportion of primary preys on a cell should decrease, thus reducing the asymmetry in predation pressure on the primary prey. These few timesteps of moving and feeding between two reproduction trials then lowered the level of asymmetry in preys' predation pressure between two survival and reproduction trials. Whereas, in most mathematical models, all life events are realised at once and applied directly on the instantaneous population densities at every timesteps, with no chance for natural processes to eventually smooth the asymmetries out.

Importantly, the removal policies resulting in the most stable predator-prey dynamics drove the predator to very low densities in the few generations following the implementation of the policy before increasing in density again. Low densities are known to make populations more vulnerable to extinction due to environmental or human-induced perturbations, particularly through Allee effects (Stephens and Sutherland, 1999; Wittmer, Sinclair and McLellan, 2005; Ng'weno *et al.*, 2019), which are defined by negative growth rate at low densities. Although negative growth rate at low densities emerged in my simulations, the Allee effect might be underestimated because the reproduction process is asexual. The animals do not need to be in the same location (i.e., on the same cell) as a mate to reproduce. An agent-based approach to sexual reproduction would require two mating animals to occur on the same cell to produce offspring, which would be increasingly unlikely at low densities, at least without active behaviour to move towards neighbouring mates. I hypothesise that such a mechanism would reduce the parameter space in which the extinction risk is null for all species in the system. Sexual reproduction is the norm in most of the conservation cases involving apparent competition as it most often involves terrestrial or aerial vertebrates; it would therefore be an important addition to make to the future versions of my model.

One of the novelties of this study is that it enlarges the scope of management strategy evaluation to other species in an apparent competition system. In most of the studies reviewed for this work, the focus of the evaluation was on the endangered species only, with little attention given to the other species in the system. Although, it is common that these other species also have a conservation or economical value. In these cases, considering all the species in interaction when evaluating management strategy can avoid the rise of conservation conflicts between human stakeholders. In Courchamp, Woodroffe and Roemer (2003) study, to preserve the fox population, the complete removal of eagles is believed to be necessary, which is hardly possible without destructive methods (Roemer *et al.*, 2001; Roemer, Donlan and Courchamp, 2002), causing a conservation conflict between eagle protection and fox preservation. Another example is presented in a case of managed savanna in Kenya, involving abandoned former cattle corrals that form nutrient-rich patches, attracting both the abundant population of zebra and the endangered, emblematic, hartebeest population. Their spatial proximity makes hartebeest predation by lions more likely than usual, threatening the hartebeest population. This led managers to reconsider the lethal control of lions, previously banned for conservation purposes, setting the premises of a conservation conflict between lion protection and hartebeest conservation (Ng'weno *et al.*, 2019). These cases would benefit from a management strategy evaluation accounting for all species involved in apparent competition interactions.

Following the amplitude of the oscillations in population densities as a measure of a management strategy efficiency is not widespread, apart from studies explicitly focusing on cycles in population dynamics (Abrams, Holt and Roth, 1998; Holt and Barfield, 2003; Barraquand *et al.*, 2015). Yet, these studies show that cycles and temporal variability such as seasonality can have an important impact on the outcome of apparent competition. Besides, incorporating these cycles in management strategy evaluation, especially in adaptive management, can enhance conservation value by calibrating intervention timing more efficiently (Bach *et al.*, 2022). Adaptive management would make sense in the policies simulated in the present study, notably by avoiding the removal of animals when their density is low or increase the rate when it is high. Adjusting the removal rate to density could also avoid the problem of low predator density after the policy implementation mentioned earlier, achieving the same final efficiency by reducing both the risk of extinction for predator and potentially the amplitude of oscillations in densities, which were tied together in all three species (Figure 26).

4.5.Conclusions

This study showed that modelling animal's behaviour more mechanistically, especially individual diet preferences, reproduction, and satiation could reduce the intensity of apparent competition expected by mathematical models. The time-explicit nature of ABMs also allows for natural processes to smooth out asymmetries between key life events. This suggests that according to parameterisation, apparent competition effects might be overestimated by MMs. Also, by combining the accounting of all the species involved in apparent competition and the follow up of the oscillations in densities as a measure of efficiency, this work showed how my model can enhance management strategy evaluation. The strategies presented here are now implemented in the public version of the model and available for researchers or managers to evaluate in other cases of apparent competition.

5. General discussion

5.1.Contribution to conservation science

Although the agent-based modelling (ABM) approach can meet many of the challenges faced by biodiversity conservation, its application in management strategy evaluation (MSE) is still scarce. I contribute to the democratisation of ABMs in conservation by proposing novel agent-based decision-helping tools for two complex conservation problems: conservation conflict management and the management of species involved in apparent competition.

In Chapter 2, I question the understudied impact of managers' timing of intervention in conservation conflicts adaptive management (Sims and Finnoff, 2013; Iacona, Possingham and Bode, 2017) using the agent-based software *GMSE* (Duthie *et al.*, 2018). I propose an alternative strategy to unconditional intervention, warranting intervention only when a criterion of distance between a prediction of the managed population size and the management target is exceeded. I have implemented my 'Trajectory' strategy as a new feature of *GMSE* and evaluated it according to conservation, food security and equity objectives (Bunnefeld *et al.*, 2013; Nilsson *et al.*, 2021). Among the benefits brought by the agent-based approach was the monitoring of policy equity among members of a stakeholder group as a management outcome. This aspect of conservation conflict has been identified as having a significant impact on stakeholders' compliance with conservation policies (Rakotonarivo, Bell, *et al.*, 2021; Rakotonarivo, Jones, *et al.*, 2021), but it had not been simulated before. The evaluation showed that the Trajectory strategy can result in a more efficient, more equitable management of a conservation conflict while saving budget. This can have important implications for budget allocation, as funds are often limiting in conservation (McDonald-Madden *et al.*, 2011; Wam *et al.*, 2016; Wu *et al.*, 2021). I want to clarify here that this strategy should not be instrumentalised to reduce the funding for conservation on the basis that interventions might be less frequent. Its efficiency relies on regular and accurate, and therefore often expansive, monitoring of both population and land-users' actions, and the budget saved should be invested to improving further interventions or allocated to other cases of conservation. The Trajectory strategy is now built in the public R-package of *GMSE*, available for managers and researchers to evaluate it in different cases of conservation conflicts.

Apparent competition is known to play a key role in the structure of species communities (Holt, 1977; Abrams, Holt and Roth, 1998; Chesson and Kuang, 2008), and conservation measures can alter these indirect interactions in ways that can hardly be anticipated without complex modelling (DeCesare *et al.*, 2010; Wittmer *et al.*, 2013; Ng'weno *et al.*, 2019). Yet, there are no existing ABMs of apparent competition, despite that the agent-based approach could significantly advance researchers' understanding of both apparent competition dynamics and how management can affect them. More specifically, the impact of spatial heterogeneity in resource distribution and habitat suitability, behavioural complexity and population structure on apparent competition dynamics have been identified as needing further research (Holt and Bonsall, 2017), which are all assets of ABMs. Therefore, I introduce in Chapter 3 a novel ABM of apparent competition between multiple resources, prey and predator populations that can simulate the aforementioned mechanics. I validated the model in its simpler form with a sensitivity analysis and compared the outcomes to the existing theory of apparent competition. The model accurately simulates apparent competition as an emergent phenomenon and is now ready to be improved and expanded upon to address the knowledge gaps. In chapter 4, I evaluate different removal strategies for the management of a species endangered by apparent competition to show how my agent-based tool can be applied to management strategy evaluation. The explicit modelling of resources, spatially explicit and time explicit nature of my model challenges other studies of previously considered management strategies, highlighting different aspects of conservation in systems involving apparent competition that might have been overlooked before, including the importance of biases in predation pressure, resource availability, and the time that separates two reproduction periods or two interventions. My model is now ready to be used as decision-helping tool to evaluate removal strategies for the management of other cases of species endangered by apparent competition.

Across all data chapters, much attention has been given to enlarge the scope of management strategy evaluation to better inform policy making. In the case of conservation conflicts, I evaluated management strategies according to both conservation objectives and farmer income, as warranted by the MSE framework (Smith, Sainsbury and Stevens, 1999; Bunnefeld, Hoshino and Milner-Gulland, 2011; Nilsson *et al.*, 2021), but I also assessed the equitable repartition of costs and benefits of conservation measures between and among stakeholder groups. This is an important outcome to measure; first because it can inform on the expected level of stakeholders' compliance to the policy and, above all, because it ensures that policies have the least impact on land-users' lives and income. In the apparent competition problem, I evaluated strategies to protect an endangered species while keeping a close watch on the other species in the system. Indeed, even if the priority is to conserve the endangered species, it should not be done at the expense of the others (unless the other species are also of conservation interest). Moreover, it is common – and will likely become increasingly prevalent – that several species in a community exhibiting apparent competition interactions are of conservation interest. These kind of situations can easily lead to conflicts about which species should be given priority for protection (Courchamp, Woodroffe and Roemer, 2003; Redpath and Thirgood, 2009; Ng'weno *et al.*, 2019), thus requiring a more global evaluation of alternative strategies. Additionally, the methods I propose are not only focused on the outcome at the end of the management period considered; analyses were carried out controlling for the dynamics along the management period. Notably, the amplitude of oscillations and cycles in population dynamics, known to have a strong influence on species persistence (Abrams, Holt and Roth, 1998; Holt and Barfield, 2003; Fryxell *et al.*, 2010; Barraquand *et al.*, 2015), have received more attention. Thus, managers can select the strategies resulting in the more stable dynamics. These methods, crossed with the assets of my ABM approach, provide two novel robust and thorough MSE tools for complex conservation problems.

5.2.Progresses permitted by the ABM approach

In conservation conflict problems, the spatially explicit nature of the agent-based approach makes it possible to evaluate management strategies in which animals can be more numerous in some landscape areas than others in an unpredictable way. The heterogeneity in animals distribution on the landscape is an important aspect to simulate because it impacts the equitable repartition of costs and benefits among the farmers; perceived inequity favouring defection from conservation policies (Rakotonarivo, Bell, *et al.*, 2021; Rakotonarivo, Jones, *et al.*, 2021). Moreover, since farmers lands were also modelled explicitly, this spatial heterogeneity was often reflected in farmer decision making, because they based their budget allocation to possible actions on the density of the managed species on their land, hence generating more variability in the actions undertaken. This can greatly influence management strategy evaluation, especially with, for example, scaring policies because it causes the animal distribution on the landscape to be both heterogeneous and unpredictable (Pollard, 2018; Nilsson *et al.*, 2021). In Chapter 3 apparent competition problem, modelling the resource spatial distribution on the landscape allowed the inter-individual variability in animals resource intake to fully take hold and simulate intra-specific competition in a more mechanistic way (Grimm, 1999; DeAngelis and Grimm, 2014). Again, this resulted in heterogeneity in animals' distribution on the landscape and therefore on the distribution of prey available to the predators. These different strata cascaded into a more realistic, more mechanistic, predator functional response, which is at the core of apparent competition dynamics (Holt, 1977; Holt, Grover and Tilman, 1994). In both problems, the spatially-explicit nature of the agent-based approach permitted to evaluate alternative management strategies while the position and local densities of animals are uncertain, thus intrinsically accounting for 'model uncertainty' (Bunnefeld, Hoshino and Milner-Gulland, 2011).

The agent-based approach allows for more flexibility in the succession of events over time. It was an asset to evaluate adaptive management strategies dynamically alternating between intervention and waiting (Sims and Finnoff, 2013; Iacona, Possingham and Bode, 2017), as the call of the policy update sub model could be conditioned to monitoring at each timestep. In the apparent competition model, allowing a few timesteps of moving, feeding, and hunting between survival and reproduction trials gave the opportunity for the inter-individual variability within populations to express its potential on intra-specific competition. But more importantly, it dampened the asymmetry caused by differences in prey populations' growth rate, as predicted by Uchmański and Grimm (1996). Thereby, it reduced asymmetry in predation and in apparent competition intensity, which, by construction, could not have been predicted by mathematical models of population dynamics.

ABMs were made to simulate agent behaviour explicitly. Modelling the flexible and dynamic decision making of stakeholders is key for the success of management strategy evaluation (Schlüter *et al.*, 2012), including choice along a continuum of possible actions and the ability to make mistakes. In *GMSE*, the agent-based approach simulated potentially suboptimal but practical decision making for both managers and farmers with an ABM of artificial intelligence called genetic algorithm (Hamblin, 2013) in the form of budget allocation to a variety of possible actions with a level corresponding to the budget allocated. Moreover, the farmers were modelled as discrete agents, and they made decision independently through their own call of the genetic algorithm. This generates inter-agent variability in decision-making, allowing the evaluation of alternative strategies while acknowledging that managers do not always make the most optimal policies and that farmers do not always react as expected, thus accounting for 'implementation uncertainty' (Kamra *et al.*, 2018; Cusack *et al.*, 2020; Nilsson *et al.*, 2021). In my apparent competition ABM, the focus on animals modelling permitted the simulation of different behaviours. First, a given prey will absorb different amount of resources from the landscape at each timestep, according to resource availability and stochastic modulation. The ABM simulated that the quality of food sources can vary over time and space and that feeding sequences are not always the same. This generated inter-individual variability in resource acquisition, therefore modelling intra-specific competition for resources. Additionally, predator preference could be modelled in a more mechanistic way (ordering of the prey available on a cell by preference before catch trial sequence) while previous mathematical models simulated preference as a fixed bias in the catch rate (Courchamp, Langlais and Sugihara, 2000; Roemer, Donlan and Courchamp, 2002). Once again, this successfully accounted for model uncertainty because it simulated unpredictable variability in the population dynamics.

5.3.Future research avenues

The Trajectory strategy for the timing of intervention in the adaptive management of conservation conflicts introduced in Chapter 2 relies on regular and accurate monitoring of a managed population. But all monitoring techniques bear uncertainty (Bunnefeld, Hoshino and Milner-Gulland, 2011; Nuno, Bunnefeld and Milner-Gulland, 2013) and monitoring accuracy in often dependent on the budget invested in population surveys (Milner-Gulland, 2011). Thus, the superiority of Trajectory strategy over unconditional intervention might depend on the budget available for monitoring; an argument that could play an important role in the selection of this strategy according to cases. I believe this question should be the next step in the exploration of the efficiency of the Trajectory strategy. It would also be interesting to investigate the pertinence of this strategy when actions other than culling are available to farmers, such as offspring control or non-destructive methods like scaring (Pollard, 2018; Nilsson *et al.*, 2021). Since they are expected to affect population density less drastically, the distance to target warranting intervention might need to be adapted accordingly.

One advantage of the Trajectory strategy is that small, inconsequential oscillations around a target will not warrant an unnecessary and potentially harmful intervention. Also, Chapter 3 and 4 demonstrated that oscillations and cycles are common in multi-species dynamics, especially in predator prey dynamics (Abrams, Holt and Roth, 1998; Holt and Barfield, 2003; Fryxell *et al.*, 2010; Barraquand *et al.*, 2015). This suggests that applying adaptive management would be most relevant to the removal strategies evaluated in Chapter 4, most likely by allowing the removal rates to change according to the monitored species densities (Bunnefeld *et al.*, 2013; Cusack *et al.*, 2020; Nilsson *et al.*, 2021). This could dampen the amplitude of cycles in population dynamics and ensure more stable dynamics. Therefore, the management of species endangered by apparent competition could benefit from the Trajectory strategy. Besides, cases of apparent competition management often generate conservation conflicts (Thirgood *et al.*, 2000; Courchamp, Woodroffe and Roemer, 2003; Redpath and Thirgood, 2009; Barraquand *et al.*, 2015; Ng'weno *et al.*, 2019), but studies of management strategy evaluation in such cases are scarce. Thus, future work might incorporate my model of apparent competition into software such as *GMSE*. For now, *GMSE* includes only one population in the resource operating model, but it is coded in a very flexible way, and the agent-based structure of both models will facilitate integration.

Now that my model of apparent competition is validated and tested in its essential version, additional progresses can be made in AC theory and related management strategy evaluation by sequentially introducing and testing features lacking understanding (Holt and Bonsall, 2017). I believe that the features to be prioritised for implementation include spatial heterogeneity in resource distribution and habitat suitability. Indeed, these are especially susceptible to be affected by conservation intervention, e.g., through the setup of supplementary feeding sites (Redpath, Thirgood and Leckie, 2001; Krofel and Jerina, 2016), the installation of fences restricting access to some but not all species (Kaswamila, Russell and McGibbon, 2007; Rocío A. Pozo *et al.*, 2021), or by providing refuges to a protected species (Sinclair *et al.*, 1998; Forrester and Steele, 2004; Jensen, Wisz and Madsen, 2008). Moreover, these kinds of management strategies have caused several conservation conflicts (Ng'weno *et al.*, 2019; Rocío A. Pozo *et al.*, 2021), hence the need to manage them with extra care. I have developed and coded the model such that these characteristics can be added as a new landscape layer, each cell having a custom value for resource abundance or accessibility to a given species.

However, I suspect that for these spatially explicit features to fully express their potential on AC dynamics, the model will need to integrate options for more active behaviour from the animals. Notably, active movement towards areas offering more resources or prey (Schmitz and Booth, 1997), towards the areas offering shelter from predation (or a more simple mechanism of predator-avoiding movement), or towards potential mates. Indeed, I believe that the option for sexual reproduction is an important feature to add to the model, as it can play an important role in the strength of Allee effects at low densities (Stephens and Sutherland, 1999; Wittmer, Sinclair and McLellan, 2005; Berec, Angulo and Courchamp, 2007; Ng'weno *et al.*, 2019). Nevertheless, these mechanisms might need more advance coding skills than adding a new characteristic to the landscape cells.

Before increasing its complexity, this exciting coding work needs to be made accessible to non-modelling users, by setting up a graphical user interface (GUI) for parameter setting and simulation, but most likely by transforming the model into an R-package to combine running simulations and automated analyses.

Indeed, a key area of improvement for most complex models resides in the bridge between developing efficient modelling tools and having stakeholders practically engage with them. First, the assumptions and hypotheses underlying a model of a socio-ecological system, or how they can effectively mimic real-world systems, are not always clear to stakeholders, which can hinder their confidence in the predictions. Especially, I believe, when they involve mathematical equations that can be daunting to a non-familiar audience. On this side, in my opinion, the assumptions of ABMs are much easier to grasp because they are much closer to individual-level animal or human mechanisms that anyone can observe, especially local land-users. Also, regardless of model complexity, parameterising, running, analysing, and communicating results from a model often requires basic modelling skills that managers do not always possess. This might require a specific position for someone having these skills in biodiversity managements teams. Focusing on parameterisation, even if higher-level parameter values can partly be found in the literature, the accurate simulation of particular cases with ABMs often requires estimating parameter values from field measurements. Not only can it be expensive and bears its own uncertainty, but parameters are often designed to ease model programming and interpretation rather than facilitate the estimation of their value from the field. I have tried to keep this in mind when programming, but it can be challenging to conciliate it with computational efficiency. The caveat of this is that the parameters can become too abstract to stakeholders, further impacting their confidence in the model. There is matter for debate because, on the one hand, models should be developed in cooperation with stakeholders to guarantee their understanding and engagement with them, and on the other hand, conservation cannot afford to design an entirely new model for every single case, but rather need flexible software that can be parameterised to a large panel of cases.

5.4. Conclusions

This thesis contributes to conservation science by taking advantage of the agent-based modelling (ABM) ability to simulate more complex and more intricate interactions between human stakeholders, animals, and their environment than the mathematical models historically used in conservation. Using ABMs in management strategy evaluation (MSE), I address two complex conservation challenges: conservation conflict (CC) management and the management of species involved in apparent competition (AC). While investigating the impact of managers' timing of intervention in CCs, I propose the "Trajectory" timing strategy, which can enhance conservation success and equity among stakeholders while offering efficient, budget-saving alternatives. My multi-species, multi-layer, ABM of AC, validated through sensitivity analysis and comparisons with existing theory and actual cases, questions and expands our understanding of the mechanisms underlying AC; especially through its individualised foraging behaviour, and time and spatially explicit structure. The model was designed to ease the inclusion and the study of more intricate low-level mechanisms influencing AC outcomes that are directly influenced by conservation interventions and are hardly simulated by usual models (e.g., complex foraging, reproductive behaviours, heterogeneity in resources repartition and accessibility). I also show how to use this model to assess removal strategies for species endangered by apparent competition, revealing insights potentially missed in previous studies, mostly involving usual mathematical models. These contributions expand the scope of management strategy evaluation, considering equity, multiple species, and oscillation dynamics, and offer uncertainty-robust agent-based tools for complex conservation problems. I hope that these tools will help further improving conservation success in an equitable way.

Literature cited

Abrams, P. (1980) ‘Are Competition Coefficients Constant? Inductive Versus Deductive Approaches’, *The American Naturalist*, 116(5), pp. 730–735.

Abrams, P.A. (1998) ‘High Competition with Low Similarity and Low Competition with High Similarity: Exploitative and Apparent Competition in Consumer-Resource Systems’, *The American Naturalist*, 152(1), pp. 114–128. Available at: https://doi.org/10.1086/286153.

Abrams, P.A., Holt, R.D. and Roth, J.D. (1998) ‘Apparent Competition or Apparent Mutualism? Shared Predation When Populations Cycle’, *Ecology*, 79(1), pp. 201–212. Available at: https://doi.org/10.1890/0012-9658(1998)079[0201:ACOAMS]2.0.CO;2.

Allesina, S. and Tang, S. (2012) ‘Stability criteria for complex ecosystems’, *Nature*, 483(7388), pp. 205–208. Available at: https://doi.org/10.1038/nature10832.

Ayllón, D. *et al.* (2016) ‘InSTREAM-Gen: Modelling eco-evolutionary dynamics of trout populations under anthropogenic environmental change’, *Ecological Modelling*, 326, pp. 36–53. Available at: https://doi.org/10.1016/j.ecolmodel.2015.07.026.

Bach, A. *et al.* (2022) ‘Intervene or wait? A model evaluating the timing of intervention in conservation conflicts adaptive management under uncertainty’, *Ecology and Society*, 27(3). Available at: https://doi.org/10.5751/ES-13341-270303.

Bainbridge, I. (2017) ‘Goose management in Scotland: An overview’, *Ambio*, 46(2), pp. 224–230. Available at: https://doi.org/10.1007/s13280-016-0883-5.

Barraquand, F. *et al.* (2015) ‘Indirect effects of primary prey population dynamics on alternative prey’, *Theoretical Population Biology*, 103, pp. 44–59. Available at: https://doi.org/10.1016/j.tpb.2015.04.002.

Behr, D.M., Ozgul, A. and Cozzi, G. (2017) ‘Combining human acceptance and habitat suitability in a unified socio-ecological suitability model: a case study of the wolf in Switzerland’, *Journal of Applied Ecology*, 54(6), pp. 1919–1929. Available at: https://doi.org/10.1111/1365-2664.12880.

Bennett, E.M. *et al.* (2015) ‘Linking biodiversity, ecosystem services, and human well-being: three challenges for designing research for sustainability’, *Current Opinion in Environmental Sustainability*, 14, pp. 76–85. Available at: https://doi.org/10.1016/j.cosust.2015.03.007.

Berec, L., Angulo, E. and Courchamp, F. (2007) ‘Multiple Allee effects and population management’, *Trends in Ecology & Evolution*, 22(4), pp. 185–191. Available at: https://doi.org/10.1016/j.tree.2006.12.002.

Bocedi, G. *et al.* (2014) ‘RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species’ responses to environmental changes’, *Methods in Ecology and Evolution*, 5(4), pp. 388–396. Available at: https://doi.org/10.1111/2041-210X.12162.

Bocedi, G. *et al.* (2021) ‘RangeShifter 2.0: an extended and enhanced platform for modelling spatial eco-evolutionary dynamics and species’ responses to environmental changes’, *Ecography*, 44(10), pp. 1453–1462. Available at: https://doi.org/10.1111/ecog.05687.

Bonsall, M.B. and Hassell, M.P. (1997) ‘Apparent competition structures ecological assemblages’, *Nature*, 388(6640), pp. 371–373. Available at: https://doi.org/10.1038/41084.

Bonsall, M.B. and Hassell, M.P. (2000) ‘The effects of metapopulation structure on indirect interactions in host-parasitoid assemblages’, *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1458), pp. 2207–2212. Available at: https://doi.org/10.1098/rspb.2000.1270.

Bouchoucha, M. *et al.* (2016) ‘Potential use of marinas as nursery grounds by rocky fishes: insights from four Diplodus species in the Mediterranean’, *Marine Ecology Progress Series*, 547, pp. 193–209. Available at: https://doi.org/10.3354/meps11641.

Bouchoucha, M. (2016) ‘Rôle des ports dans le cycle de vie des poissons. Les ports : nurseries de sars ?’ Available at: https://archimer.ifremer.fr/doc/00345/45635/ (Accessed: 19 March 2023).

Bousquet, F. and Le Page, C. (2004) ‘Multi-agent simulations and ecosystem management: a review’, *Ecological Modelling*, 176(3), pp. 313–332. Available at: https://doi.org/10.1016/j.ecolmodel.2004.01.011.

ten Broeke, G., van Voorn, G. and Ligtenberg, A. (2016) ‘Which Sensitivity Analysis Method Should I Use for My Agent-Based Model?’, *Journal of Artificial Societies and Social Simulation*, 19(1), p. 5.

Bunnefeld, N. *et al.* (2013) ‘Incentivizing Monitoring and Compliance in Trophy Hunting’, *Conservation Biology*, 27(6), pp. 1344–1354. Available at: https://doi.org/10.1111/cobi.12120.

Bunnefeld, N., Hoshino, E. and Milner-Gulland, E.J. (2011) ‘Management strategy evaluation: a powerful tool for conservation?’, *Trends in Ecology & Evolution*, 26(9), pp. 441–447. Available at: https://doi.org/10.1016/j.tree.2011.05.003.

Caswell, H. (1988) ‘Theory and models in ecology: A different perspective’, *Ecological Modelling*, 43(1), pp. 33–44. Available at: https://doi.org/10.1016/0304-3800(88)90071-3.

Ceballos, G., Ehrlich, P.R. and Dirzo, R. (2017) ‘Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines’, *Proceedings of the National Academy of Sciences*, 114(30), pp. E6089–E6096. Available at: https://doi.org/10.1073/pnas.1704949114.

Chapman, D.S. *et al.* (2009) ‘Modelling the coupled dynamics of moorland management and upland vegetation’, *Journal of Applied Ecology*, 46(2), pp. 278–288. Available at: https://doi.org/10.1111/j.1365-2664.2009.01618.x.

Chesson, P. (2000) ‘Mechanisms of Maintenance of Species Diversity’, *Annual Review of Ecology and Systematics*, 31(1), pp. 343–366. Available at: https://doi.org/10.1146/annurev.ecolsys.31.1.343.

Chesson, P. and Kuang, J.J. (2008) ‘The interaction between predation and competition’, *Nature*, 456(7219), pp. 235–238. Available at: https://doi.org/10.1038/nature07248.

Colyvan, M., Justus, J. and Regan, H.M. (2011) ‘The conservation game’, *Biological Conservation*, 144(4), pp. 1246–1253. Available at: https://doi.org/10.1016/j.biocon.2010.10.028.

Costanza, R. *et al.* (1997) ‘The value of the world’s ecosystem services and natural capital’, *Nature*, 387(6630), pp. 253–260. Available at: https://doi.org/10.1038/387253a0.

Côté, I.M. and Sutherland, W.J. (1997) ‘The Effectiveness of Removing Predators to Protect Bird Populations’, *Conservation Biology*, 11(2), pp. 395–405. Available at: https://doi.org/10.1046/j.1523-1739.1997.95410.x.

Courchamp, F., Langlais, M. and Sugihara, G. (1999) ‘Cats protecting birds: modelling the mesopredator release effect’, *Journal of Animal Ecology*, 68(2), pp. 282–292. Available at: https://doi.org/10.1046/j.1365-2656.1999.00285.x.

Courchamp, F., Langlais, M. and Sugihara, G. (2000) ‘Rabbits killing birds: modelling the hyperpredation process’, *Journal of Animal Ecology*, 69(1), pp. 154–164. Available at: https://doi.org/10.1046/j.1365-2656.2000.00383.x.

Courchamp, F., Woodroffe, R. and Roemer, G. (2003) ‘Removing Protected Populations to Save Endangered Species’, *Science* [Preprint]. Available at: https://doi.org/10.1126/science.1089492.

Cusack, J. *et al.* (2020) ‘Integrating conflict, lobbying, and compliance to predict the sustainability of natural resource use’, *Ecology and Society*, 25(2). Available at: https://doi.org/10.5751/ES-11552-250213.

DeAngelis, D.L. and Grimm, V. (2014) ‘Individual-based models in ecology after four decades’, *F1000Prime Reports*, 6, p. 39. Available at: https://doi.org/10.12703/P6-39.

DeAngelis, D.L. and Yurek, S. (2017a) ‘Spatially Explicit Modeling in Ecology: A Review’, *Ecosystems*, 20(2), pp. 284–300. Available at: https://doi.org/10.1007/s10021-016-0066-z.

DeAngelis, D.L. and Yurek, S. (2017b) ‘Spatially Explicit Modeling in Ecology: A Review’, *Ecosystems*, 20(2), pp. 284–300. Available at: https://doi.org/10.1007/s10021-016-0066-z.

DeCesare, N.J. *et al.* (2010) ‘Endangered, apparently: the role of apparent competition in endangered species conservation’, *Animal Conservation*, 13(4), pp. 353–362. Available at: https://doi.org/10.1111/j.1469-1795.2009.00328.x.

Du Toit, J.T. (2010) ‘Considerations of scale in biodiversity conservation’, *Animal Conservation*, 13(3), pp. 229–236. Available at: https://doi.org/10.1111/j.1469-1795.2010.00355.x.

Duthie, A.B. *et al.* (2018) ‘GMSE: An r package for generalised management strategy evaluation’, *Methods in Ecology and Evolution*, 9(12), pp. 2396–2401. Available at: https://doi.org/10.1111/2041-210X.13091.

Forrester, G.E. and Steele, M.A. (2004) ‘Predators, Prey Refuges, and the Spatial Scaling of Density-Dependent Prey Mortality’, *Ecology*, 85(5), pp. 1332–1342. Available at: https://doi.org/10.1890/03-0184.

Fryxell, J.M. *et al.* (2010) ‘Resource Management Cycles and the Sustainability of Harvested Wildlife Populations’, *Science*, 328(5980), pp. 903–906. Available at: https://doi.org/10.1126/science.1185802.

Game, E.T. *et al.* (2014) ‘Conservation in a Wicked Complex World; Challenges and Solutions’, *Conservation Letters*, 7(3), pp. 271–277. Available at: https://doi.org/10.1111/conl.12050.

Glynatsi, N.E., Knight, V. and Lee, T.E. (2018) 'An evolutionary game theoretic model of rhino horn devaluation', *Ecological Modelling*, 389, pp. 33–40. Available at: https://doi.org/10.1016/j.ecolmodel.2018.10.003.

Gordon, A. *et al.* (2011) 'Assessing the impacts of biodiversity offset policies', *Environmental Modelling & Software*, 26(12), pp. 1481–1488. Available at: https://doi.org/10.1016/j.envsoft.2011.07.021.

Grainger, T.N., Levine, J.M. and Gilbert, B. (2019) 'The Invasion Criterion: A Common Currency for Ecological Research', *Trends in Ecology & Evolution*, 34(10), pp. 925–935. Available at: https://doi.org/10.1016/j.tree.2019.05.007.

Gregory, R., Ohlson, D. and Arvai, J. (2006) 'Deconstructing Adaptive Management: Criteria for Applications to Environmental Management', *Ecological Applications*, 16(6), pp. 2411–2425. Available at: https://doi.org/10.1890/1051-0761(2006)016[2411:DAMCFA]2.0.CO;2.

Grimm, V. (1999) 'Ten years of individual-based modelling in ecology: what have we learned and what could we learn in the future?', *Ecological Modelling*, 115(2), pp. 129–148. Available at: https://doi.org/10.1016/S0304-3800(98)00188-4.

Grimm, V. *et al.* (2006) 'A standard protocol for describing individual-based and agent-based models', *Ecological Modelling*, 198(1), pp. 115–126. Available at: https://doi.org/10.1016/j.ecolmodel.2006.04.023.

Grimm, V. *et al.* (2010) 'The ODD protocol: A review and first update', *Ecological Modelling*, 221(23), pp. 2760–2768. Available at: https://doi.org/10.1016/j.ecolmodel.2010.08.019.

Grimm, V. *et al.* (2020) 'The ODD Protocol for Describing Agent-Based and Other Simulation Models: A Second Update to Improve Clarity, Replication, and Structural Realism', *Journal of Artificial Societies and Social Simulation*, 23(2), p. 7.

Hamblin, S. (2013) 'On the practical usage of genetic algorithms in ecology and evolution', *Methods in Ecology and Evolution*, 4(2), pp. 184–194. Available at: https://doi.org/10.1111/2041-210X.12000.

Hart, S.P., Freckleton, R.P. and Levine, J.M. (2018) 'How to quantify competitive ability', *Journal of Ecology*, 106(5), pp. 1902–1909. Available at: https://doi.org/10.1111/1365-2745.12954.

Hauert, C., Holmes, M. and Doebeli, M. (2006) 'Evolutionary games and population dynamics: maintenance of cooperation in public goods games', *Proceedings of the Royal Society B: Biological Sciences*, 273(1600), pp. 2565–2571. Available at: https://doi.org/10.1098/rspb.2006.3600.

Hautier, Y. *et al.* (2015) 'Anthropogenic environmental changes affect ecosystem stability via biodiversity', *Science*, 348(6232), pp. 336–340. Available at: https://doi.org/10.1126/science.aaa1788.

Heinonen, J.P.M. and Travis, J.M.J. (2015) 'Modelling conservation conflicts', in J.C. Young et al. (eds) *Conflicts in Conservation: Navigating Towards Solutions*. Cambridge: Cambridge University Press (Ecological Reviews), pp. 195–211. Available at: https://doi.org/10.1017/CBO9781139084574.015.

Hicks, L.L. *et al.* (2009) 'Chapter 21 - Plum Creek's Central Cascades Habitat Conservation Plan and Modeling for the Northern Spotted Owl', in J.J. Millspaugh and F.R. Thompson (eds)

Models for Planning Wildlife Conservation in Large Landscapes. San Diego: Academic Press, pp. 561–592. Available at: https://doi.org/10.1016/B978-0-12-373631-4.00021-6.

Hilbe, C. *et al.* (2018) 'Evolution of cooperation in stochastic games', *Nature*, 559(7713), pp. 246–249. Available at: https://doi.org/10.1038/s41586-018-0277-x.

Holt, R.D. (1977) 'Predation, apparent competition, and the structure of prey communities', *Theoretical Population Biology*, 12(2), pp. 197–229. Available at: https://doi.org/10.1016/0040-5809(77)90042-9.

Holt, R.D. and Barfield, M. (2003) 'Impacts of temporal variation on apparent competition and coexistence in open ecosystems', *Oikos*, 101(1), pp. 49–58. Available at: https://doi.org/10.1034/j.1600-0706.2003.12570.x.

Holt, R.D. and Bonsall, M.B. (2017) 'Apparent Competition', *Annual Review of Ecology, Evolution, and Systematics*, 48(1), pp. 447–471. Available at: https://doi.org/10.1146/annurev-ecolsys-110316-022628.

Holt, R.D., Grover, J. and Tilman, D. (1994) 'Simple Rules for Interspecific Dominance in Systems with Exploitative and Apparent Competition', *The American Naturalist*, 144(5), pp. 741–771. Available at: https://doi.org/10.1086/285705.

Holt, R.D. and Lawton, J.H. (1993) 'Apparent Competition and Enemy-Free Space in Insect Host-Parasitoid Communities', *The American Naturalist* [Preprint]. Available at: https://doi.org/10.1086/285561.

Hughey, K.F.D., Cullen, R. and Moran, E. (2003) 'Integrating Economics into Priority Setting and Evaluation in Conservation Management', *Conservation Biology*, 17(1), pp. 93–103. Available at: https://doi.org/10.1046/j.1523-1739.2003.01317.x.

Iacona, G.D., Possingham, H.P. and Bode, M. (2017) 'Waiting can be an optimal conservation strategy, even in a crisis discipline', *Proceedings of the National Academy of Sciences*, 114(39), pp. 10497–10502. Available at: https://doi.org/10.1073/pnas.1702111114.

Jachowski, D.S. and Kesler, D.C. (2009) 'Allowing extinction: should we let species go?', *Trends in Ecology & Evolution*, 24(4), p. 180. Available at: https://doi.org/10.1016/j.tree.2008.11.006.

Jacobs, J. (1974) 'Quantitative measurement of food selection', *Oecologia*, 14(4), pp. 413–417. Available at: https://doi.org/10.1007/BF00384581.

Jensen, R.A., Wisz, M.S. and Madsen, J. (2008) 'Prioritizing refuge sites for migratory geese to alleviate conflicts with agriculture', *Biological Conservation*, 141(7), pp. 1806–1818. Available at: https://doi.org/10.1016/j.biocon.2008.04.027.

Judson, O.P. (1994) 'The rise of the individual-based model in ecology', *Trends in Ecology & Evolution*, 9(1), pp. 9–14. Available at: https://doi.org/10.1016/0169-5347(94)90225-9.

Kamra, N. *et al.* (2018) 'Policy Learning for Continuous Space Security Games Using Neural Networks', *Proceedings of the AAAI Conference on Artificial Intelligence*, 32(1). Available at: https://doi.org/10.1609/aaai.v32i1.11446.

Kaswamila, A., Russell, S. and McGibbon, M. (2007) 'Impacts of Wildlife on Household Food Security and Income in Northeastern Tanzania', *Human Dimensions of Wildlife*, 12(6), pp. 391–404. Available at: https://doi.org/10.1080/10871200701670003.

Keith, D.A. *et al.* (2011) ‘Uncertainty and adaptive management for biodiversity conservation’, *Biological Conservation*, 144(4), pp. 1175–1178. Available at: https://doi.org/10.1016/j.biocon.2010.11.022.

Kell, L.T. *et al.* (2007) ‘FLR: an open-source framework for the evaluation and development of management strategies’, *ICES Journal of Marine Science*, 64(4), pp. 640–646. Available at: https://doi.org/10.1093/icesjms/fsm012.

Krofel, M. and Jerina, K. (2016) ‘Mind the cat: Conservation management of a protected dominant scavenger indirectly affects an endangered apex predator’, *Biological Conservation*, 197, pp. 40–46. Available at: https://doi.org/10.1016/j.biocon.2016.02.019.

Leslie, P.H. (1945) ‘On the Use of Matrices in Certain Population Mathematics’, *Biometrika*, 33(3), pp. 183–212. Available at: https://doi.org/10.2307/2332297.

Lotka, A.J. (1920) ‘Analytical Note on Certain Rhythmic Relations in Organic Systems’, *Proceedings of the National Academy of Sciences*, 6(7), pp. 410–415. Available at: https://doi.org/10.1073/pnas.6.7.410.

Mahévas, S. and Pelletier, D. (2004) ‘ISIS-Fish, a generic and spatially explicit simulation tool for evaluating the impact of management measures on fisheries dynamics’, *Ecological Modelling*, 171(1), pp. 65–84. Available at: https://doi.org/10.1016/j.ecolmodel.2003.04.001.

Mason, T.H.E., Keane, A., *et al.* (2018) ‘The changing environment of conservation conflict: Geese and farming in Scotland’, *Journal of Applied Ecology*, 55(2), pp. 651–662. Available at: https://doi.org/10.1111/1365-2664.12969.

Mason, T.H.E., Pollard, C.R.J., *et al.* (2018) ‘Wicked conflict: Using wicked problem thinking for holistic management of conservation conflict’, *Conservation Letters*, 11(6), p. e12460. Available at: https://doi.org/10.1111/conl.12460.

McDonald-Madden, E. *et al.* (2011) ‘Allocating conservation resources between areas where persistence of a species is uncertain’, *Ecological Applications*, 21(3), pp. 844–858. Available at: https://doi.org/10.1890/09-2075.1.

McDonald-Madden, E., Baxter, P.W.J. and Possingham, H.P. (2008) ‘Making robust decisions for conservation with restricted money and knowledge’, *Journal of Applied Ecology*, 45(6), pp. 1630–1638. Available at: https://doi.org/10.1111/j.1365-2664.2008.01553.x.

McPeek, M.A. (2019) ‘Mechanisms influencing the coexistence of multiple consumers and multiple resources: resource and apparent competition’, *Ecological Monographs*, 89(1), p. e01328. Available at: https://doi.org/10.1002/ecm.1328.

Milner-Gulland, E.J. (2011) ‘Integrating fisheries approaches and household utility models for improved resource management’, *Proceedings of the National Academy of Sciences*, 108(4), pp. 1741–1746. Available at: https://doi.org/10.1073/pnas.1010533108.

Morris, R.J., Lewis, O.T. and Godfray, H.C.J. (2005) ‘Apparent competition and insect community structure: towards a spatial perspective’, *Annales Zoologici Fennici*, 42(4), pp. 449–462.

Mouquet, N. *et al.* (2005) ‘Conserving Community Modules: A Case Study of the Endangered Lycaenid Butterfly Maculinea Alcon’, *Ecology*, 86(12), pp. 3160–3173. Available at: https://doi.org/10.1890/04-1664.

Myerson, R.B. (1991) *Game Theory: Analysis of Conflict*. Harvard University Press. Available at: https://doi.org/10.2307/j.ctvjsf522.

Ng'weno, C.C. *et al.* (2019) 'Apparent Competition, Lion Predation, and Managed Livestock Grazing: Can Conservation Value Be Enhanced?', *Frontiers in Ecology and Evolution*, 7. Available at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00123 (Accessed: 2 February 2023).

Nicol, S. *et al.* (2019) 'Quantifying the impact of uncertainty on threat management for biodiversity', *Nature Communications*, 10(1), p. 3570. Available at: https://doi.org/10.1038/s41467-019-11404-5.

Nilsson, L. *et al.* (2021) 'Effects of stakeholder empowerment on crane population and agricultural production', *Ecological Modelling*, 440, p. 109396. Available at: https://doi.org/10.1016/j.ecolmodel.2020.109396.

Nuno, A., Bunnefeld, N. and Milner-Gulland, E.J. (2013) 'Matching observations and reality: using simulation models to improve monitoring under uncertainty in the Serengeti', *Journal of Applied Ecology*, 50(2), pp. 488–498. Available at: https://doi.org/10.1111/1365-2664.12051.

Nyhus, P.J. (2016) 'Human–Wildlife Conflict and Coexistence', *Annual Review of Environment and Resources*, 41(1), pp. 143–171. Available at: https://doi.org/10.1146/annurev-environ-110615-085634.

Oliver, M., Luque-Larena, J.J. and Lambin, X. (2009) 'Do rabbits eat voles? Apparent competition, habitat heterogeneity and large-scale coexistence under mink predation', *Ecology Letters*, 12(11), pp. 1201–1209. Available at: https://doi.org/10.1111/j.1461-0248.2009.01375.x.

Orrock, J.L., Holt, R.D. and Baskett, M.L. (2010) 'Refuge-mediated apparent competition in plant–consumer interactions', *Ecology Letters*, 13(1), pp. 11–20. Available at: https://doi.org/10.1111/j.1461-0248.2009.01412.x.

Pérez, P., Ruiz-Herrera, A. and San Luis, A.M. (2020) 'Management guidelines in disturbance-Prone populations: The importance of the intervention time', *Journal of Theoretical Biology*, 486, p. 110075. Available at: https://doi.org/10.1016/j.jtbi.2019.110075.

Pollard, C.R.J. (2018) 'The role of social interactions in conservation conflict: goose management across Scotland'. Available at: http://dspace.stir.ac.uk/handle/1893/30324 (Accessed: 11 February 2023).

Pooley, S. *et al.* (2017) 'An interdisciplinary review of current and future approaches to improving human–predator relations', *Conservation Biology*, 31(3), pp. 513–523. Available at: https://doi.org/10.1111/cobi.12859.

Pozo, Rocío A. *et al.* (2021) 'A multispecies assessment of wildlife impacts on local community livelihoods', *Conservation Biology*, 35(1), pp. 297–306. Available at: https://doi.org/10.1111/cobi.13565.

Pozo, R. A. *et al.* (2021) 'Reconciling livestock production and wild herbivore conservation: challenges and opportunities', *Trends in Ecology & Evolution*, 36(8), pp. 750–761. Available at: https://doi.org/10.1016/j.tree.2021.05.002.

R core team (2022) ‘R: A Language and Environment for Statistical Computing’. Vienna, Austria: R Foundation for Statistical Computing. Available at: https://www.R-project.org/.

Railsback, S.F., Ayllón, D. and Harvey, B.C. (2021) ‘InSTREAM 7: Instream flow assessment and management model for stream trout’, *River Research and Applications*, 37(9), pp. 1294–1302. Available at: https://doi.org/10.1002/rra.3845.

Rakotonarivo, O.S., Jones, I.L., *et al.* (2021) ‘Experimental evidence for conservation conflict interventions: The importance of financial payments, community trust and equity attitudes’, *People and Nature*, 3(1), pp. 162–175. Available at: https://doi.org/10.1002/pan3.10155.

Rakotonarivo, O.S., Bell, A., *et al.* (2021) ‘The role of incentive-based instruments and social equity in conservation conflict interventions’, *Ecology and Society*, 26(2). Available at: https://doi.org/10.5751/ES-12306-260208.

Redpath, S. and Thirgood, S. (2009) ‘Hen harriers and red grouse: moving towards consensus?’, *Journal of Applied Ecology*, 46(5), pp. 961–963. Available at: https://doi.org/10.1111/j.1365-2664.2009.01702.x.

Redpath, S.M. *et al.* (2013) ‘Understanding and managing conservation conflicts’, *Trends in Ecology & Evolution*, 28(2), pp. 100–109. Available at: https://doi.org/10.1016/j.tree.2012.08.021.

Redpath, S.M. *et al.* (eds) (2015) *Conflicts in Conservation: Navigating Towards Solutions*. Cambridge: Cambridge University Press (Ecological Reviews). Available at: https://doi.org/10.1017/CBO9781139084574.

Redpath, S.M., Thirgood, S.J. and Leckie, F.M. (2001) ‘Does supplementary feeding reduce predation of red grouse by hen harriers?’, *Journal of Applied Ecology*, 38(6), pp. 1157–1168. Available at: https://doi.org/10.1046/j.0021-8901.2001.00683.x.

Richardson, S. *et al.* (2020) ‘A systematic review of adaptive wildlife management for the control of invasive, non-native mammals, and other human–wildlife conflicts’, *Mammal Review*, 50(2), pp. 147–156. Available at: https://doi.org/10.1111/mam.12182.

Roemer, G.W. *et al.* (2001) ‘Feral pigs facilitate hyperpredation by golden eagles and indirectly cause the decline of the island fox’, *Animal Conservation*, 4(4), pp. 307–318. Available at: https://doi.org/10.1017/S1367943001001366.

Roemer, G.W., Donlan, C.J. and Courchamp, F. (2002) ‘Golden eagles, feral pigs, and insular carnivores: How exotic species turn native predators into prey’, *Proceedings of the National Academy of Sciences*, 99(2), pp. 791–796. Available at: https://doi.org/10.1073/pnas.012422499.

Rosenzweig, M.L. and MacArthur, R.H. (1963) ‘Graphical Representation and Stability Conditions of Predator-Prey Interactions’, *The American Naturalist*, 97(895), pp. 209–223. Available at: https://doi.org/10.1086/282272.

Ruiz-Miranda, C.R., Vilchis, L.I. and Swaisgood, R.R. (2020) ‘Exit strategies for wildlife conservation: why they are rare and why every institution needs one’, *Frontiers in Ecology and the Environment*, 18(4), pp. 203–210. Available at: https://doi.org/10.1002/fee.2163.

Schlüter, M. *et al.* (2012) ‘New Horizons for Managing the Environment: A Review of Coupled Social-Ecological Systems Modeling’, *Natural Resource Modeling*, 25(1), pp. 219–272. Available at: https://doi.org/10.1111/j.1939-7445.2011.00108.x.

Schmitz, O.J. and Booth, G. (1997) ‘Modelling food web complexity: The consequences of individual-based, spatially explicit behavioural ecology on trophic interactions’, *Evolutionary Ecology*, 11(4), pp. 379–398. Available at: https://doi.org/10.1023/A:1018476606256.

Serrouya, R. *et al.* (2015) ‘Using Predator-Prey Theory to Predict Outcomes of Broadscale Experiments to Reduce Apparent Competition’, *The American Naturalist*, 185(5), pp. 665–679. Available at: https://doi.org/10.1086/680510.

Sims, C. and Finnoff, D. (2013) ‘When is a “wait and see” approach to invasive species justified?’, *Resource and Energy Economics*, 35(3), pp. 235–255. Available at: https://doi.org/10.1016/j.reseneeco.2013.02.001.

Sinclair, A.R.E. *et al.* (1998) ‘Predicting Effects of Predation on Conservation of Endangered Prey’, *Conservation Biology*, 12(3), pp. 564–575. Available at: https://doi.org/10.1111/j.1523-1739.1998.97030.x.

Smith, A.D.M., Sainsbury, K.J. and Stevens, R.A. (1999) ‘Implementing effective fisheries-management systems – management strategy evaluation and the Australian partnership approach’, *ICES Journal of Marine Science*, 56(6), pp. 967–979. Available at: https://doi.org/10.1006/jmsc.1999.0540.

Smith, J.M. and Price, G.R. (1973) ‘The Logic of Animal Conflict’, *Nature*, 246(5427), pp. 15–18. Available at: https://doi.org/10.1038/246015a0.

Smith, L.M. and Hall, S. (2016) ‘Extended leaf phenology may drive plant invasion through direct and apparent competition’, *Oikos*, 125(6), pp. 839–848. Available at: https://doi.org/10.1111/oik.02529.

Steffen, W. *et al.* (2015) ‘Planetary boundaries: Guiding human development on a changing planet’, *Science*, 347(6223), p. 1259855. Available at: https://doi.org/10.1126/science.1259855.

Stephens, P.A. and Sutherland, W.J. (1999) ‘Consequences of the Allee effect for behaviour, ecology and conservation’, *Trends in Ecology & Evolution*, 14(10), pp. 401–405. Available at: https://doi.org/10.1016/S0169-5347(99)01684-5.

Stillman, R.A. (2008) ‘MORPH—An individual-based model to predict the effect of environmental change on foraging animal populations’, *Ecological Modelling*, 216(3), pp. 265–276. Available at: https://doi.org/10.1016/j.ecolmodel.2008.04.014.

Stillman, R.A. *et al.* (2015) ‘Making Predictions in a Changing World: The Benefits of Individual-Based Ecology’, *BioScience*, 65(2), pp. 140–150. Available at: https://doi.org/10.1093/biosci/biu192.

Sundararaj, V. *et al.* (2012) ‘Can rare positive interactions become common when large carnivores consume livestock?’, *Ecology*, 93(2), pp. 272–280. Available at: https://doi.org/10.1890/10-2050.1.

Termansen, M. *et al.* (2019) ‘Chapter Four - Modelling land use dynamics in socio-ecological systems: A case study in the UK uplands’, in D.A. Bohan and A.J. Dumbrell (eds) *Advances in Ecological Research*. Academic Press (Resilience in Complex Socio-ecological Systems), pp. 125–152. Available at: https://doi.org/10.1016/bs.aecr.2019.03.002.

Thiele, J.C. (2014) ‘R Marries NetLogo: Introduction to the RNetLogo Package’, *Journal of Statistical Software*, 58, pp. 1–41. Available at: https://doi.org/10.18637/jss.v058.i02.

Thiele, J.C., Kurth, W. and Grimm, V. (2014) ‘Facilitating Parameter Estimation and Sensitivity Analysis of Agent-Based Models: A Cookbook Using NetLogo and R’, *Journal of Artificial Societies and Social Simulation*, 17(3), p. 11.

Thirgood, S. *et al.* (2000) ‘Raptors and Red Grouse: Conservation Conflicts and Management Solutions’, *Conservation Biology*, 14(1), pp. 95–104. Available at: https://doi.org/10.1046/j.1523-1739.2000.99013.x.

Tilman, A.R., Watson, J.R. and Levin, S. (2017) ‘Maintaining cooperation in social-ecological systems’:, *Theoretical Ecology*, 10(2), pp. 155–165. Available at: https://doi.org/10.1007/s12080-016-0318-8.

Uchmański, J. and Grimm, V. (1996) ‘Individual-based modelling in ecology: what makes the difference?’, *Trends in Ecology & Evolution*, 11(10), pp. 437–441. Available at: https://doi.org/10.1016/0169-5347(96)20091-6.

Volterra, V. (1926) ‘Fluctuations in the Abundance of a Species considered Mathematically1’, *Nature*, 118(2972), pp. 558–560. Available at: https://doi.org/10.1038/118558a0.

Walters, C.J. (1986) *Adaptive Management of Renewable Resources*. Basingstoke: Macmillan Publishers Ltd. Available at: https://iiasa.dev.local/ (Accessed: 10 March 2023).

Wam, H.K. *et al.* (2016) ‘Conflicting interests of ecosystem services: Multi-criteria modelling and indirect evaluation of trade-offs between monetary and non-monetary measures’, *Ecosystem Services*, 22, pp. 280–288. Available at: https://doi.org/10.1016/j.ecoser.2016.10.003.

van Wilgen, B.W. and Biggs, H.C. (2011) ‘A critical assessment of adaptive ecosystem management in a large savanna protected area in South Africa’, *Biological Conservation*, 144(4), pp. 1179–1187. Available at: https://doi.org/10.1016/j.biocon.2010.05.006.

Williams, B.K., Johnson, F.A. and Wilkins, K. (1996) ‘Uncertainty and the Adaptive Management of Waterfowl Harvests’, *The Journal of Wildlife Management*, 60(2), pp. 223–232. Available at: https://doi.org/10.2307/3802220.

Wittmer, H.U. *et al.* (2007) ‘Changes in landscape composition influence the decline of a threatened woodland caribou population’, *Journal of Animal Ecology*, 76(3), pp. 568–579. Available at: https://doi.org/10.1111/j.1365-2656.2007.01220.x.

Wittmer, H.U. *et al.* (2013) ‘Conservation Strategies for Species Affected by Apparent Competition’, *Conservation Biology*, 27(2), pp. 254–260. Available at: https://doi.org/10.1111/cobi.12005.

Wittmer, H.U., Elbroch, L.M. and Marshall, A.J. (2013) ‘Good intentions gone wrong: did conservation management threaten Endangered huemul deer Hippocamelus bisulcus in the future Patagonia National Park?’, *Oryx*, 47(3), pp. 393–402. Available at: https://doi.org/10.1017/S0030605312000531.

Wittmer, H.U., Sinclair, A.R.E. and McLellan, B.N. (2005) ‘The role of predation in the decline and extirpation of woodland caribou’, *Oecologia*, 144(2), pp. 257–267. Available at: https://doi.org/10.1007/s00442-005-0055-y.

Wu, C.-H. *et al.* (2021) ‘Reallocating budgets among ongoing and emerging conservation projects’, *Conservation Biology*, 35(3), pp. 955–966. Available at: https://doi.org/10.1111/cobi.13585.

Zurell, D. *et al.* (2010) 'The virtual ecologist approach: simulating data and observers', *Oikos*, 119(4), pp. 622–635. Available at: https://doi.org/10.1111/j.1600-0706.2009.18284.x.

Appendices

A1. Chapter 2 - Modelling details

Model overview

Model case.

To simulate conservation conflict management over time, we develop an individual-based model with a population of discrete animals, discrete farmers, and a biodiversity manager, all interacting on an agricultural landscape. The landscape is divided into discrete cells, each of which produces an agricultural yield and can hold any number of animals. Each farmer owns a contiguous block of cells that forms their 'land', and the sum of its cells' productivity determines the farmer's yield. Each animal's reproduction and survival depend on the amount of agricultural resources it consumes from landscape cells, which consequently reduces the farmers' yield. Farmers can cull animals that are on their own land to reduce yield loss. We chose population parameter values to ensure that unrestricted culling consistently drove the animal population to extinction (see the 'initial parameters' section below). The manager attempts to avoid extinction by maintaining the population around a predefined target size (T_N). This target was chosen to be high enough to prevent extinction, but low enough to ensure a satisfactory yield to farmers. The manager's method is to implement a policy incentivizing or disincentivizing culling as appropriate to increase or decrease population size to be closer to T_N. Hence, following an adaptive management process, the manager updates this policy according to the monitoring of the population size (N_t) at each timestep t. Farmers' and manager's actions are constrained by finite budgets (respectively B_F and B_M), which we interpret to reflect the total time, energy or money that a farmer can allocate to realize culling actions, or the manager to implement a change of policy and enforce culling restrictions at each timestep. Furthermore, a conservation conflict will arise when the policy enforced by the manager prevents the farmers from culling as many animals as they want to minimize yield loss. Our case's conflict dynamics are therefore affected by both the ecology of the population and the flexible, goal-oriented decision-making of the manager and farmers.

Manager policymaking.

To maintain the population as close as possible to T_N, the manager receives a fixed, non-cumulative budget B_M at the beginning of each timestep (i.e., it is completely lost if unused at the end of the timestep). They can allocate it into setting a cost that farmers must pay to cull an animal on their land. A minimum cost of 10 budget units (b.u.) models the baseline budget needed for a farmer to cull an animal. The manager can draw into B_M to raise this cost to discourage farmers from culling and favor population growth and can decrease it to facilitate culling and favor a population decrease. To model the budget needed to enforce a policy restricting culling, a raise of 1 in the culling cost requires an investment of 10 b.u. from the manager. Conversely, as the manager does not need to incentivize farmers to remove animals when the policy allows high culling rates, they do not need to spend budget to decrease the cost. The amount by which the manager changes the culling cost is computed according to their goal (see the 'decision-making sub-model' section below), i.e., keeping the population as close as possible to target. Manager's goal was modelled as minimizing the distance between the monitored population size N_t and T_N.

Timing strategies.

We included three timing strategies that determine whether a manager intervenes and updates the policy or waits and leaves it as is. The Control strategy (CTL) was the null model in this study. It corresponds to unconditional intervention at every opportunity and was modelled as the manager simply updating the policy at every timestep. With the Adaptive Timing of Intervention strategy (ATI), the manager dynamically alternates between intervening and waiting based on the distance between N_t and T_N. ATI defines a permissive range P_T around T_N in the form of $T_N \pm P_T$. Within this range, the manager considers N_t close enough to T_N, and consequently, that the current policy results in a sustainable culling rate for the population. Hence, at a given timestep, the manager will update the policy if and only if the population is monitored outside this $T_N \pm P_T$ range. The Trajectory (TRJ) strategy is the same as the ATI strategy, except that when N_t is into $T_N \pm P_T$, the manager makes a prediction on next timestep's population size based on the current and preceding monitoring results. If this prediction falls into the $T_N \pm P_T$ range, the manager assumes that the policy is effective and leaves it unchanged; otherwise, they update it. In both ATI and TRJ strategies, after a timestep without updating the policy, the manager receives an additional proportion B_b of B_M to model the benefits associated with waiting (e.g., the money, time or energy saved by not engaging in the process of updating the policy and enforce the change on farmers, or the interests gained from putting up the money saved). This bonus can be accumulated over several consecutive timesteps of waiting but is lost as soon as the manager draws into their budget to raise the level of restrictions again.

Farmers' action planning.

At the beginning of each timestep, each farmer receives a fixed, non-cumulative budget B_F, which they allocate into culling a certain number of animals on the land that they own at the cost set by the manager's policy. The number of animal culled is independently computed for each farmer using *GMSE*'s evolutionary algorithm (see the 'decision-making sub-model' section below), meaning that each farmer makes an independent decision for how to act according to their goal: maximizing their own yield. We used this model case to investigate how different timing strategies for a biodiversity manager's intervention can affect the outcomes of an adaptively managed conservation conflict.

Simulations with *GMSE*

To simulate a conservation conflict management with different strategies under uncertainty, we used the R package '*GMSE*' (Duthie et al. 2018). *GMSE* is a flexible modelling tool to simulate key aspects of natural resource management over time and address adaptive management questions *in silico* (Cusack et al. 2020, Nilsson et al. 2021). *GMSE* offers a range of parameters to simulate resource variations and management policy options with individual-based models of population dynamics, monitoring, manager decision-making and farmer decision-making.

Initial parameters.

We modelled a spatially explicit landscape with a grid of 200 by 200 cells, divided into 40 equally sized rectangular pieces of land, each individually owned by one of 40 farmers. For the animals, we wanted to model a population that is stable in absence of culling, but under an important threat of extinction under a high culling rate. We defined the population dynamics model parameters such that, under constraint of density-dependent intra-specific resource competition only, an equilibrium was reached quickly and steadily, as a stable natural population would. The size at equilibrium (K) was sought such that the expected number of animals per farmer's land was about a hundred on average (i.e., around 4000 individuals on the landscape). The farmers were provided with an initial budget high enough to cull up to the expected number of animals on their land at the baseline cost (i.e., 1000 b.u), and at first, the manager's initial budget was set equal to the farmers' one. We set T_N at half the equilibrium size, which was low enough to maintain farmers' yield over 90% of their maximum yield, but high enough to ensure a relatively low extinction risk of around 15% with the Control strategy (c.f. Management outcomes and Results sections in main document). We intentionally chose these parameters for the Control strategy to produce adequate management while also leaving room for improvement in order to determine the extent to which alternative strategies can generate better results. We set the initial population size N_0 = 1000, which is sufficiently far below K for the population to be under extinction threat and justify the initial involvement of a manager.

Population dynamics sub-model.

GMSE's population dynamics model features a population of N animals, each of which has an age as well as an x and y landscape position, all initialized at random (integers sampled with equal probabilities along the range of possible values). In each timestep, each animal moves from its current cell to a random cell within a defined range of cells in any direction (including the original cell). After arriving at a cell, the animal feeds and consumes a proportion of 0.5 of the cell's remaining yield. All animals move 12 times during a single timestep, but individual movement across all animals occurs in a random order to avoid having a subset of animals complete all their moving and feeding before the others have started. After all movement and feeding has occurred, the animals asexually produce one offspring for every 5 resource units consumed (e.g., if an animal has consumed 12 resource units it produces 2 offspring). The offspring are added to the population as new individuals of age 0 on the cell on which they were produced. Next, animals that have consumed over 4.75 resource units and have an age under or equal to 5 timesteps survive to the next one. Animals that do not survive are removed from the population. This consumption criteria lead to density-dependent intra-specific competition for resource, and modelling life events discretely and probabilistically generates inter-individual variability, as well as geographical and demographic stochasticity, therefore accounting for several sources of uncertainty around population dynamics.

Monitoring sub-model.

We assumed that the manager makes no errors during monitoring, thus N_t represents the exact population size at each timestep. This assumption avoided modelled stochastic monitoring errors that would have challenged a full understanding of management dynamics.

Decision-making sub-model.

Manager and farmer decision-making is modelled in *GMSE* using evolutionary algorithms (Hamblin 2012). Each time an agent makes a decision, the *GMSE* evolutionary algorithm generates a set of random possible policies for managers (culling costs) or action plans for farmers (number of culls), and then allows this set to evolve on its own self-contained timescale. Policies or action plans that are better aligned to an agent's goal have a relatively high fitness, and the fittest ones are selected to be the agent's policy/action plan when the conditions for the algorithm termination are met (see supporting information S1 in Duthie et al. 2018, and *GMSE* documentation for further details). Our model thereby computes a practical but not necessarily optimal decision, recognizing that most people cannot think of every single possibility to choose the optimal one, but can choose the best option among those they could conceive. This process generates inter-individual variability, errors, and stochasticity in agents' decision-making, therefore simulating several sources of uncertainty around human behavior.

Timing strategies implementation.

CTL is the default strategy in *GMSE*: at each timestep t, the evolutionary algorithm calculates an appropriate cost of culling (most likely a raise in the cost when $N_t < T_N$ and a decrease when $N_t > T_N$). In contrast, when applying ATI, the manager updates the policy only if N_t is out of the permissive range ($T_N \pm P_T$). Hence, the evolutionary algorithm is called only if

$$\left|\frac{N_t}{T_N} - 1\right| > P_T$$

Otherwise, the cost is left the same as the previous timestep. Lastly, when applying TRJ, the process is the same as ATI, except that the decision to update is based on a prediction of next timestep's population size $\widehat{N}_{t+1}$ instead of N_t. We chose as a predicting function a simple linear extrapolation based on the current (N_t) and previous (N_{t-1}) population sizes that has the advantage of including the influence of the active policy on population variation in a simple way. Hence, with TRJ the condition for calling the evolutionary algorithm is

$$\left|\frac{\widehat{N}_{t+1}}{T_N} - 1\right| > P_T ,$$

With $\widehat{N}_{t+1} = N_t + (N_t - N_{t-1})$.

Otherwise, the cost stays the same as previous timestep. After a timestep without calling the evolutionary algorithm, the manager starts the next one with an addition of a proportion B_b of B_M b.u. to their regular budget B_M. (See Fig. A5 for a flowchart of the different strategies.)

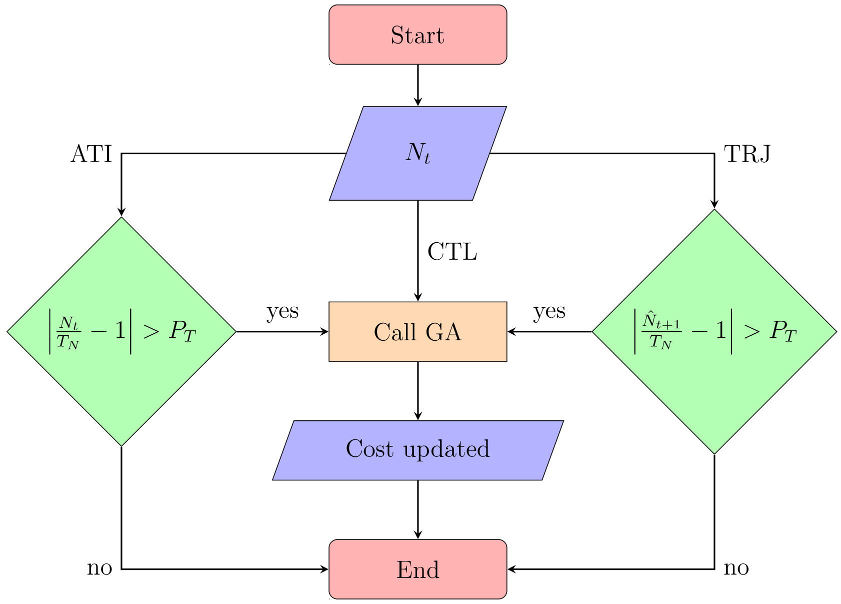

Figure A1. Flowchart of the three timing strategies.

Table A1.1. Summary of useful symbols.

Symbol	Status	Description	Unit
t_{max}	constant	max simulation time	times steps
T_N	constant	manager's target for population size	nb. of individuals
N_0	constant	initial population size	nb. of individuals
N_t	variable	population size monitored at timestep t	nb. of individuals
P_T	variable	permissiveness around T_N	% of T_N
B_M	variable	manager's initial budget	b.u.
B_b	variable	budget bonus amount	% of B_M
f_{ext}	outcome	extinction frequency over a set of replicates	% of replicates
Y_{end}	outcome	average farmers' yield at the end of a simulation.	% of landscape max productivity
Y_{ineq}	outcome	average differential between lowest and highest farmers' yields at the end of a simulation	% of highest yield
d_T	outcome	Average distance between Nt and T_N at the end of a simulation	% of T_N
t_w	outcome	Average proportion of timesteps without intervention	% of simulation time

Table A1.2. *GMSE* parameter values. Parameters not mentioned here were set to default (as in https://confoobio.github.io/*GMSE*/articles/SI3.html).

Parameter	Value	Description
time_max	20	Maximum timesteps in simulation
land_dim1	200	Width of landscape (horizontal cells)
land_dim2	200	Length of landscape
res_death_type	0	Rules affecting resource death (consumption-based)
res_birth_type	0	Rules affecting resource birth (consumption-based)
observe_type	3	Type of resource observation (transect observation)
res_move_obs	FALSE	Resource move during transect observation
res_consume	0.5	Pr. of a landscape cell's value reduced by the presence of a resource in a timestep
max_ages	5	The maximum number of timesteps a resource can persist before it is removed
minimumcost	10	The minimum cost of a farmer performing culling
user_budget	1000	A farmer's budget per timestep for performing any number of actions
manager_budget	1000	A manager's budget per timestep for setting policy
manage_target	2000	The manager's target resource abundance
RESOURCE_init	1000	The initial abundance of resources
culling	TRUE	Resource culling (removes a resource entirely) is a policy option
stakeholders	40	Number of farmers in the simulation
landownership	TRUE	farmers own land and increase utility indirectly from landscape instead of resource use
manager_sense	0.15	A metric of managers accuracy in predicting change in stakeholder behaviour given a change in cost
consume_surv	4.75	Amount of cell value for a resource to eventually survive until the next timestep
consume_repr	5	Amount of cell value for a resource to eventually produce offspring
times_feeding	12	Maximum number of times a resource consumes landscape value per timestep

A2. Chapter 2 - Additional figures of the adaptive timing of intervention strategy experiment results.

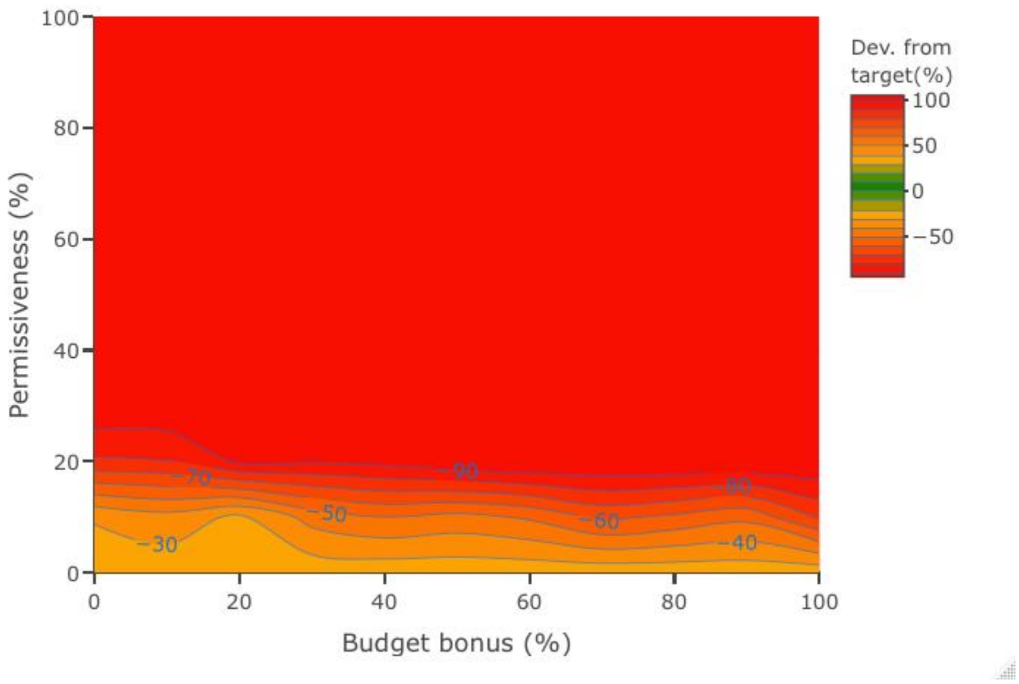

Figure A2.1. Population's average deviation from target (d_T) at the final timestep of simulation according to permissiveness (P_T) and budget bonus (B_b) values when applying the Adaptive Timing of Intervention strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the closer the population to manager's target (T_N). Given the numerous extinctions (see Fig.1), the population very often ended at a size of 0, meaning a –100% deviation from target, hence the large red area. With Control strategy, the population was under target by –30 to –20%. Expectedly, this reflects the same tendency as the extinction frequency f_{ext}.

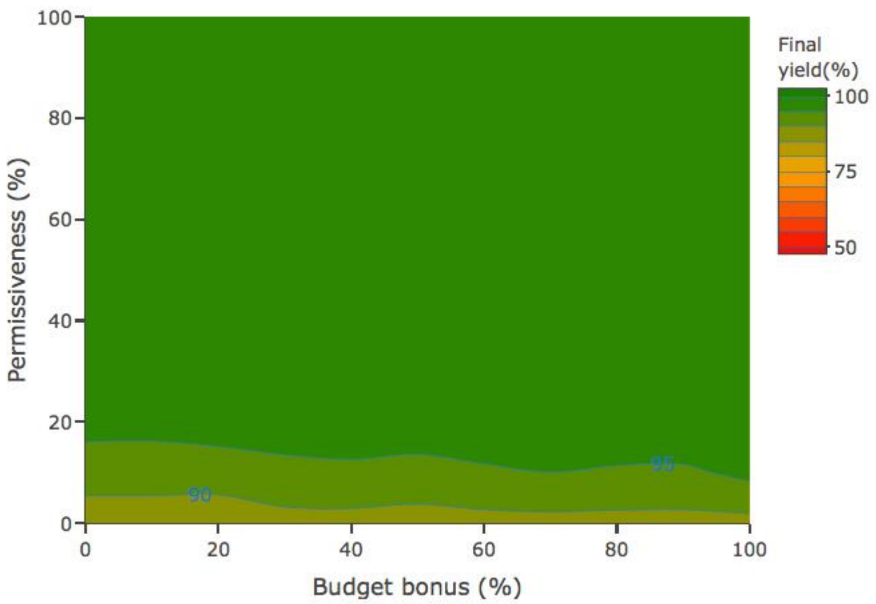

Figure A2.2. Average farmers' yield (Y_{end}) at the final timestep of simulation according to permissiveness (P_T) and budget bonus (B_b) values when applying the Adaptive Timing of Intervention strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the closer the farmers' yield to landscape maximal productivity. Given the numerous extinctions (see Fig.1), farmers very often reach their maximal yield, hence the large green area. With control strategy, farmers got between 85 and 90% of their maximal yield on average because the population was more efficiently managed and thus larger.

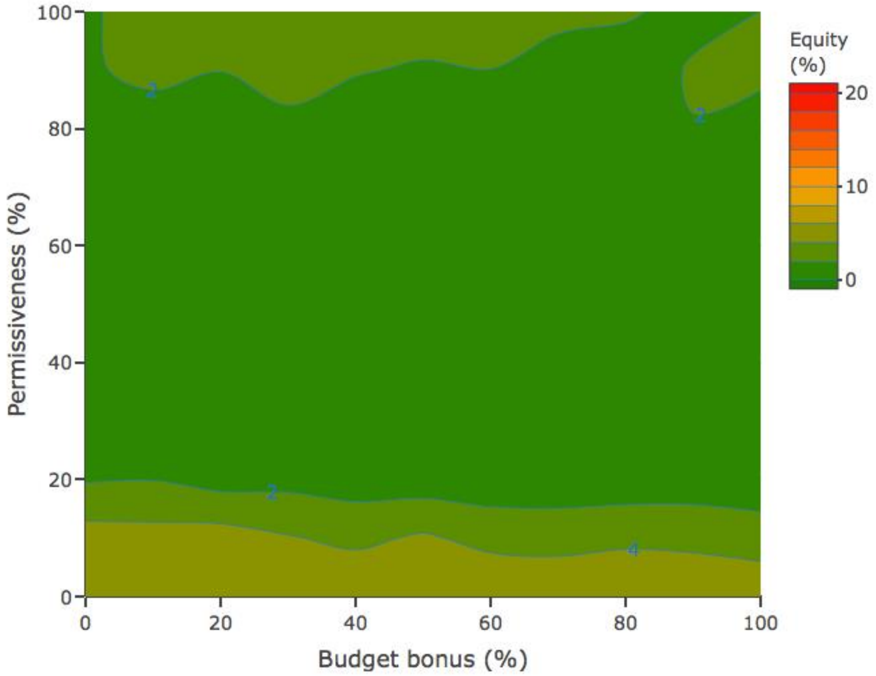

Figure A2.3. Average farmers' yield inequity (Y_{ineq}) at the final timestep of simulation according to permissiveness (P_T) and budget bonus (B_b) values when applying the Adaptive Timing of Intervention strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the smaller the difference between the highest and lowest farmer's yields. Given the numerous extinctions (see Fig.1), farmers very often reach their maximal yield while the lower yields were higher than with control strategy, hence the very low inequity.

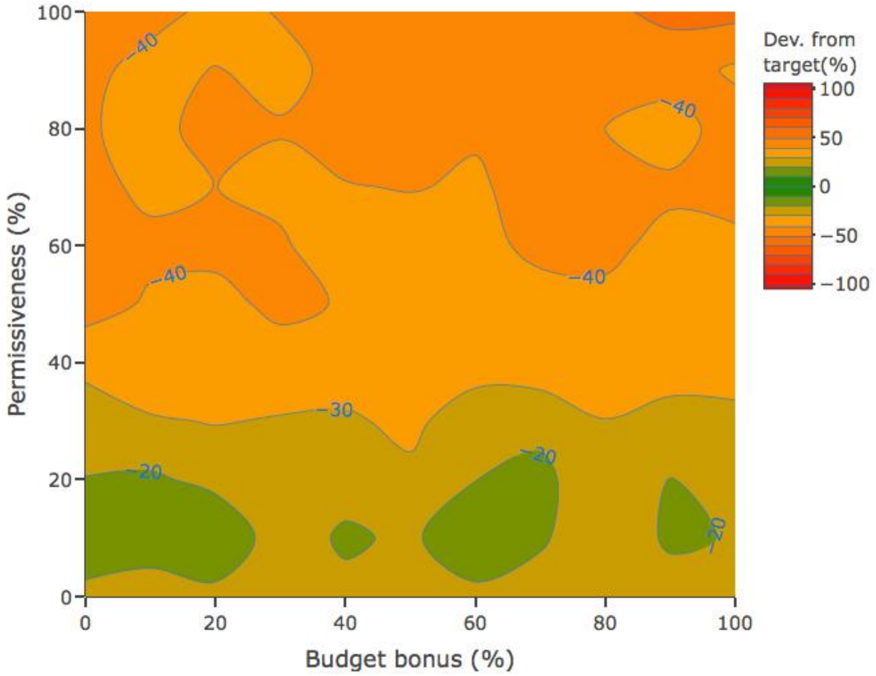

Figure A2.4. Population's average deviation from target (d_T) at the timestep before the end of simulation (t_{max} or extinction) according to permissiveness (P_T) and budget bonus (B_b) values. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the closer the population to manager's target (T_N). Note that in most areas of high extinction risk (red areas in Fig.1), the population size was monitored into the corresponding permissive range in the timestep preceding extinction, causing the manager to wait when intervention was urgent.

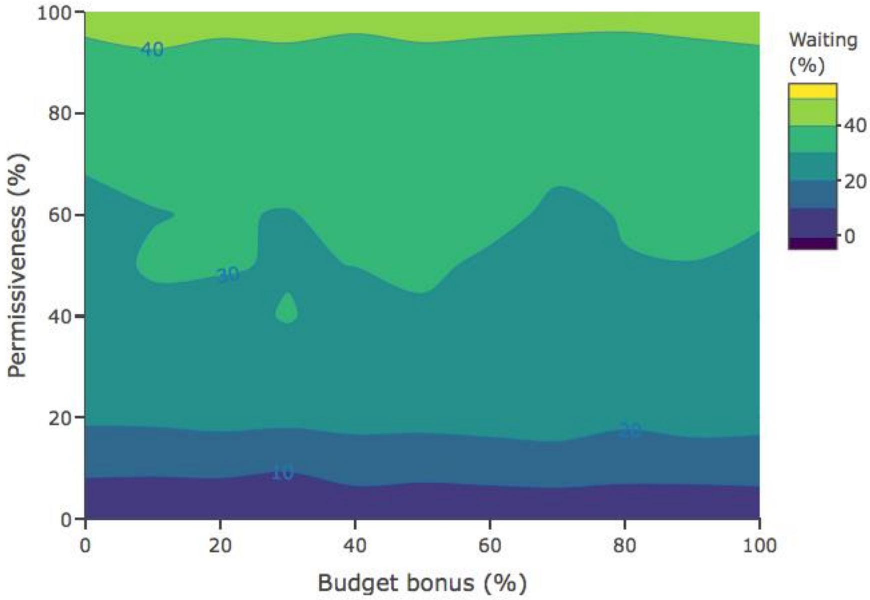

Figure A2.5. Average proportion of timesteps without manager's intervention (t_w) during a simulation according to permissiveness (P_T) and budget bonus (B_b) values when applying the adaptive timing of intervention strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The lighter, the larger the number of timesteps without intervention.

A3. Chapter 2 - Additional figures of the trajectory strategy experiment results

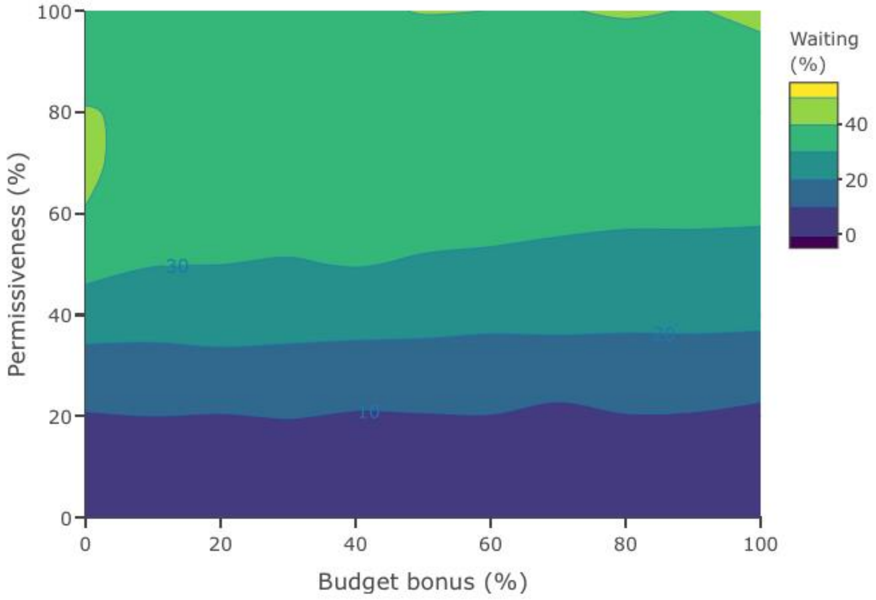

Figure A3.1. Average proportion of timesteps without manager's intervention (t_w) during a simulation according to permissiveness (P_T) and budget bonus (B_b) values when applying the Trajectory strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The lighter, the larger the number of timesteps without intervention. In the 30% P_T parameter area, the manager could save between 10 and 20% of their interventions.

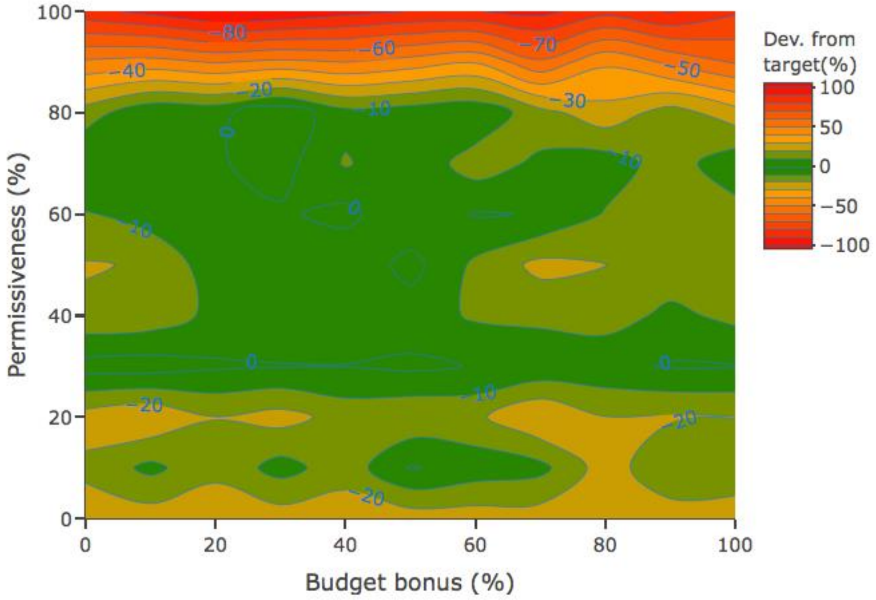

Figure A3.2. Population's average deviation from target (d_T) at the final timestep of simulation according to permissiveness (P_T) and budget bonus (B_b) values when applying the Trajectory strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the closer the population to manager's target (T_N). Most areas are greener than the control strategy (P_T = 0 band) meaning that the trajectory strategy maintained the population closer to target. Note that in the P_T = 30 parameter area, d_T is the closest to 0 for every B_b values.

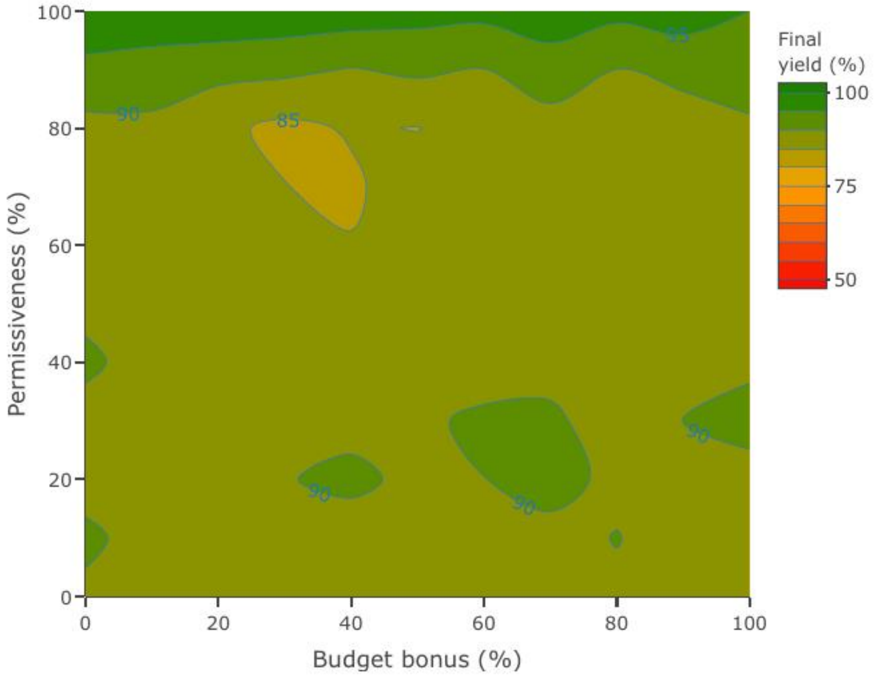

Figure A3.3. Average farmers' yield (Y_{end}) at the final timestep of simulation according to permissiveness (P_T) and budget bonus (B_b) values when applying the Trajectory strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the closer the farmers' yield to landscape maximal productivity. Most areas are as green as control strategy, with a final farmers' yield over 85% of their maximum.

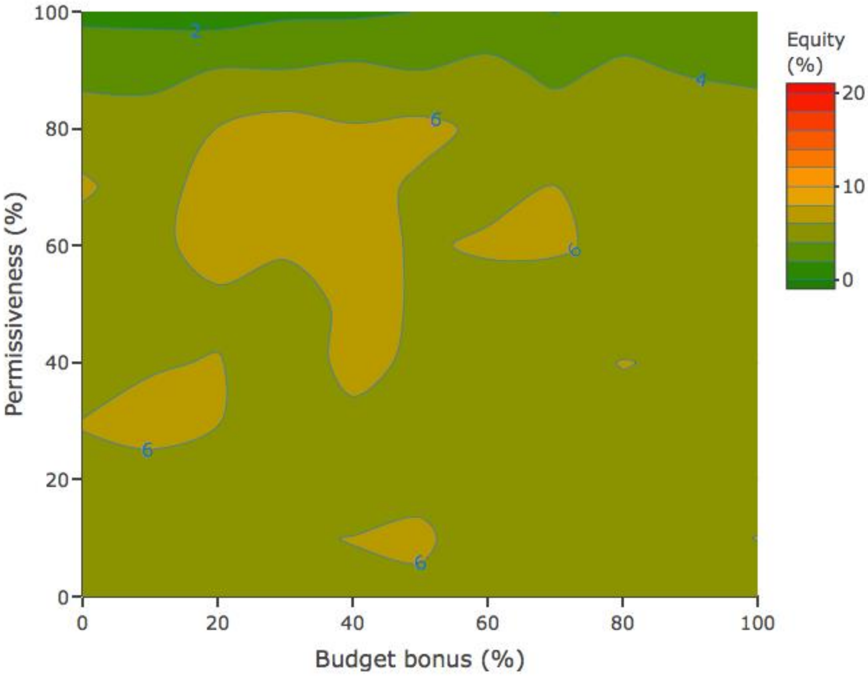

Figure A3.4. Average farmers' yield inequity (Y_{ineq}) at the final timestep of simulation according to permissiveness (P_T) and budget bonus (B_b) values when applying the trajectory strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the smaller the difference between the highest and lowest farmer's yields. Most areas are as equitable, or slightly less equitable than control strategy.

A4. Chapter 2 - Additional figures of the sensitivity to manager's initial budget experiment results

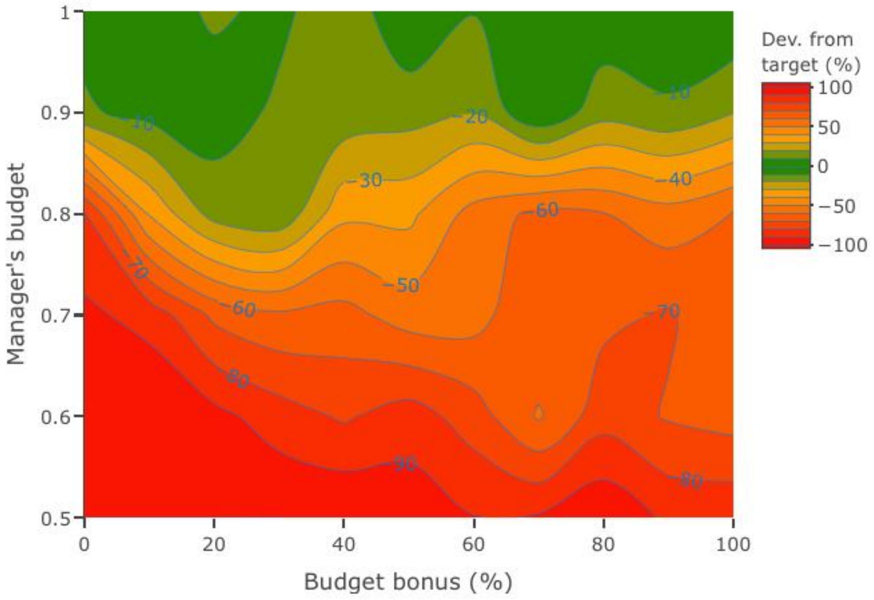

Figure A4.1. Population's average deviation from target (d_T) at the final timestep of simulation according to manager's initial budget (B_M) and budget bonus (B_b) values when applying the Trajectory strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the closer the population to manager's target (T_N).

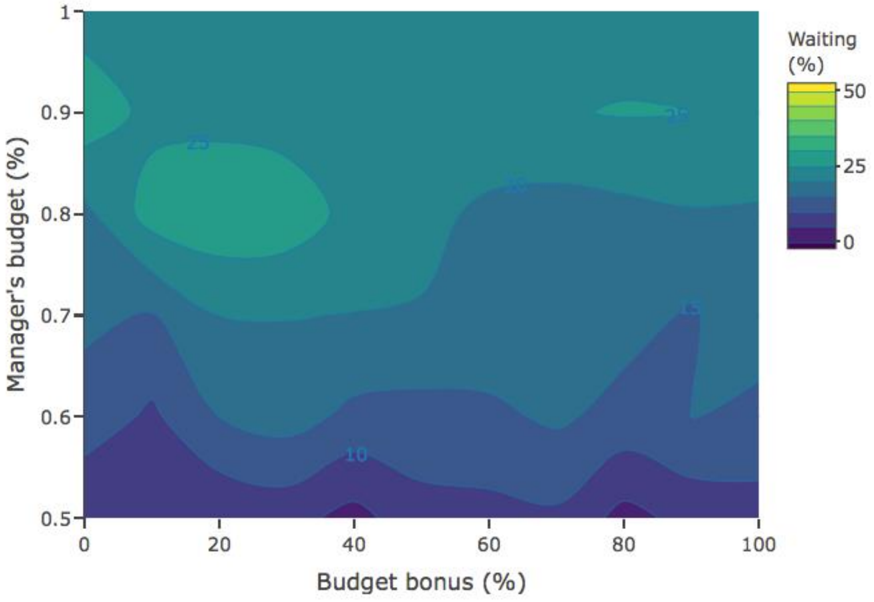

Figure A4.2. Average proportion of timesteps without manager's intervention (t_w) during a simulation according to manager's initial budget (B_M) and budget bonus (B_b) values when applying the Trajectory strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The lighter, the larger the number of timesteps without intervention. The B_M = 800 b.u. and 20-30% B_b parameter area was also the one where the manager needed to intervene less, another sign that the population is often close enough to target not to need an intervention.

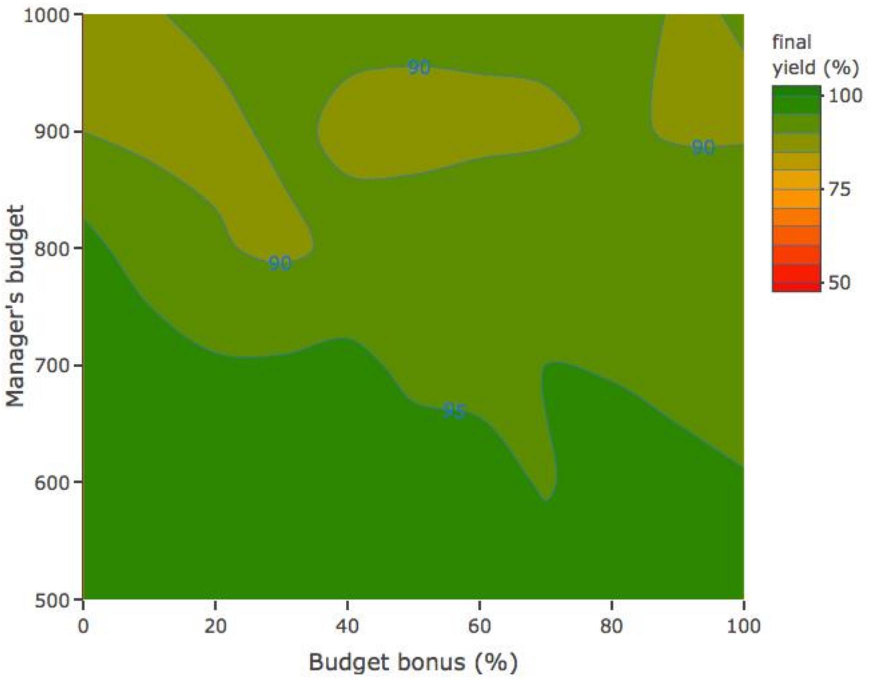

Figure A4.3. Average farmers' yield (Y_{end}) at the final timestep of simulation according to manager's initial budget (B_M) and budget bonus (B_b) values when applying the Trajectory strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the closer the farmers' yield to landscape maximal productivity. In the areas where the extinction frequency is acceptable, the farmers' final yield is over 85% of their maximum, which is comparable to the previous experiments.

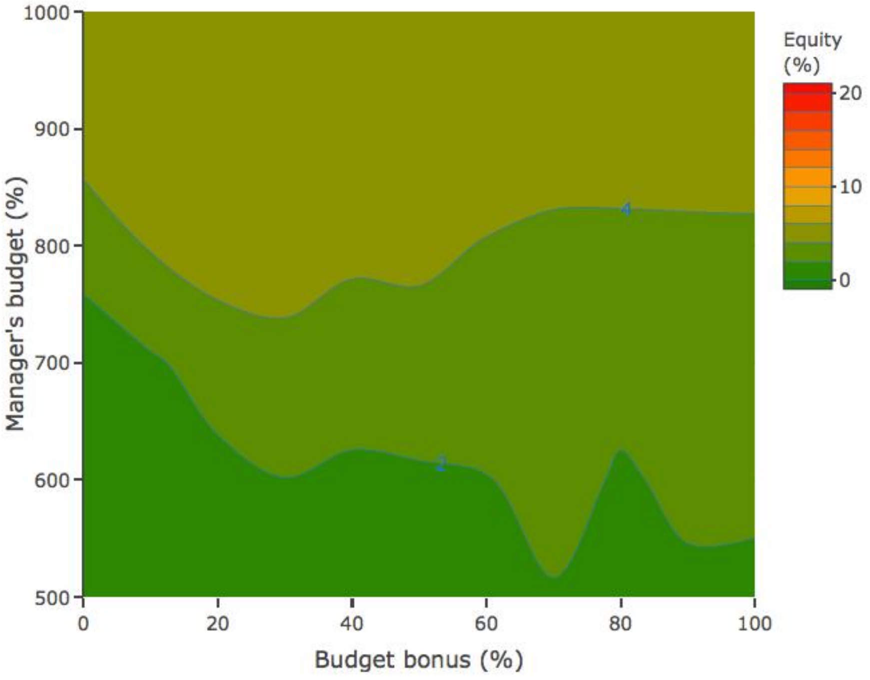

Figure A4.4. Average farmers' yield inequity (Y_{ineq}) at the final timestep of simulation according to manager's initial budget (B_M) and budget bonus (B_b) values when applying the trajectory strategy. Results from simulations with an individual-based model simulating the adaptive management of a population under conditions of conservation conflict. The greener, the smaller the difference between the highest and lowest farmer's yields. In the areas where the extinction frequency is acceptable, the inequity is between 4 and 6% which is comparable to the previous experiments.